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Bothalia is named in honour of General Louis Botha, first Premier and Minister of Agriculture of the Union of South Africa. This house journal of the National Botanical Institute, Pretoria, is devoted to the furtherance of botanical science. The main fields covered are taxonomy, ecology, anatomy and cytology. Two parts of the journal and an index to contents, authors and subjects are published annually.

Bothalia is vernoem ter ere van Generaal Louis Botha, eerste Eerste Minister en Minister van Landbou van die Unie van Suid-Afrika. Hierdie lyfblad van die Nasionale Botaniese Instituut, Pretoria, is gewy aan die bevordering van die wetenskap van plantkunde. Die hoofgebiede wat gedek word, is taksonomie, ekologie, anatomie en sitologie. Twee dele van die tydskrif en 'n indeks van die inhoud, outeurs en onderwerpe verskyn jaarliks.

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The memoirs are individual treatises usually of an ecological nature, but sometimes dealing with taxonomy or economic botany.

'n Reeks van losstaande omvattende verhandelings oor vernaamlik ekologiese, maar soms ook taksonomiese of plantekonomiese onderwerpe.

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Vanaf Vol. 50 word een deel, bestaande uit twintig plate, jaarliks gepubliseer. 'n Volume bestaan uit twee dele. Die publikasie is beskikbaar in Afrikaans en Engels.

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BOTHALIA

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Notes on the Strumariinae (Amaryllidaceae-Amaryllideae). Six new taxa in *Strumaria* and *Hessea* from the central and northwestern Cape, South Africa, and southern Namibia

D.A. SNIJMAN*

Keywords: Amaryllidaceae, Amaryllideae, *Hessea, Strumaria*, new rare species, subspecies, southern Africa

ABSTRACT

Newly described are four species and a subspecies of *Strumaria* and one species of *Hessea. S.* **aestivalis** Snijman from the Langberg and *S.* **perryae** Snijman from the Bokkeveld escarpment are rare species closely allied to *S. pubescens* W.F. Barker. *S.* **discifera** Marloth ex Snijman is widespread on the Bokkeveld and Roggeveld escarpments but *S.* **discifera** subsp. **bulbifera** Snijman which comprises several clonal populations, is narrowly restricted to the dolerite ridges near Nieuwoudtville. *S.* **villosa** Snijman, a rare species, is localised on quartz hills near Kosies in the Richtersveld. *H.* **speciosa** Snijman occurs in red sand and friable loam from southern Namibia to the central Cape.

UITTREKSEL

Vier nuwe spesies en 'n subspesie van *Strumaria* sowel as 'n nuwe *Hessea*-spesie word beskryf. *S.* **aestivalis** Snijman van die Langberg en *S.* **perryae** Snijman van die Bokkeveld platorand is skaars soorte wat na aan *S. pubescens* W.F. Barker verwant is. *S.* **discifera** Marloth ex Snijman is wydverspreid langs die Bokkeveld- en Roggeveld-platorand. *S.* **discifera** subsp. **bulbifera** Snijman is beperk tot 'n aantal klonale populasies op die doleriet-heuwels naby Nieuwoudtville. *S.* **villosa** Snijman, 'n skaars soort, word slegs op die kwartsiet-heuwels naby Kosies in die Richtersveld aangetref. *H.* **speciosa** Snijman kom voor in rooi sand en bros leem vanaf suidelike Namibië tot in die Kaapse Middellande.

INTRODUCTION

The Strumariinae, an exclusively southern African subtribe of the Amaryllideae, is centred in the semi-arid winter rainfall region of the Cape Province. The often insignificant, hysteranthous leaves and short-lived autumn flowers of the species, are phenological characteristics which render many members of the subtribe insufficiently collected. Thus since the last review of the Strumariinae (Müller-Doblies 1985) some 12 additional new taxa have been discovered, of which five have already been published (Snijman 1989; Snijman 1991).

The 37 known species of Strumariinae are currently placed in eight genera (*Namaquanula* D. & U. Müller-Doblies, *Kamiesbergia* Snijman, *Hessea* Herb., *Carpolyza* Salisb., *Strumaria* Jacq., *Bokkeveldia* D. & U. Müller-Doblies, *Gemmaria* Salisb. and *Tedingea* D. & U. Müller-Doblies). Phylogenetic studies in the Strumariinae using cladistic analyses (Snijman in prep.) have shown that *Strumaria, Bokkeveldia* and *Gemmaria* are weakly defined and paraphyletic and that they are best treated as a single genus *Strumaria*. Although the necessary generic redelimitation will be explained and effected elsewhere, it is important, notably for conservation purposes, to validate the names of the undescribed species of the subtribe. Four of the new species described here are assigned to *Strumaria*, here defined according to Ker-Gawler (1814), Bolus (1923), Barker (1943, 1944). The fifth new species is placed in *Hessea sensu* Müller-Doblies (1985), which has proven to be a monophyletic genus with the exclusion of the poorly known species *H. spiralis* Baker.

* Compton Herbarium, National Botanical Institute, Private Bag X7, Claremont 7735, South Africa.
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MATERIALS AND METHODS

This study was based on material from BM, BOL, K, NBG, PRE, SAM and WIND. Additional morphological and phenological data were gathered from the living collection of all known members of the Strumariinae at the National Botanical Garden, Kirstenbosch. Habitat information was derived from my own field observations. The dates accompanying the cited specimens are field collection dates of flowering bulbs. Specimens without dates comprise cultivated flowering material which was gathered over several years.

1. **S. aestivalis** *Snijman*, sp. nov., quoad tunicam luteam bulbi, folia pubescentia et flores infundibuliformes ad *S. pubescentem* W.F. Barker accedit, sed ab ea concavitatibus latis inter filamenta interiora et stylum differt. Figure 1.

TYPE.—Cape Province, 3018 (Kamiesberg): (—DB), Farm Langberg, NW of Loeriesfontein, fl ex NBG 31-1-1984, *Perry 1991* (NBG, holo.; K, PRE, MO).

Bulb solitary or occasionally forming bulblets, ovoid, 20–40 mm diam., with the outer fibrous covering ranging from brown to cream-coloured, fleshy and yellowish within; neck up to 70 mm long, rarely absent. *Leaves* absent at anthesis, 2 or rarely 3, recurved, lorate, 80–280 × 15–26 mm, canaliculate, both surfaces densely pubescent with 2 mm long, patent, silky, white hairs; amplexicaul cataphyll shortly exserted, tipped with red, soon withering down; non-amplexicaul prophyll hidden in the bulb. *Inflorescence* widely spreading, 60–100 mm across; scape 60–100 × 2.5–4.0 mm, pale green to glaucous, sometimes flushed with pink, pubescent or glabrous, breaking off at the base in fruit; spathe valves

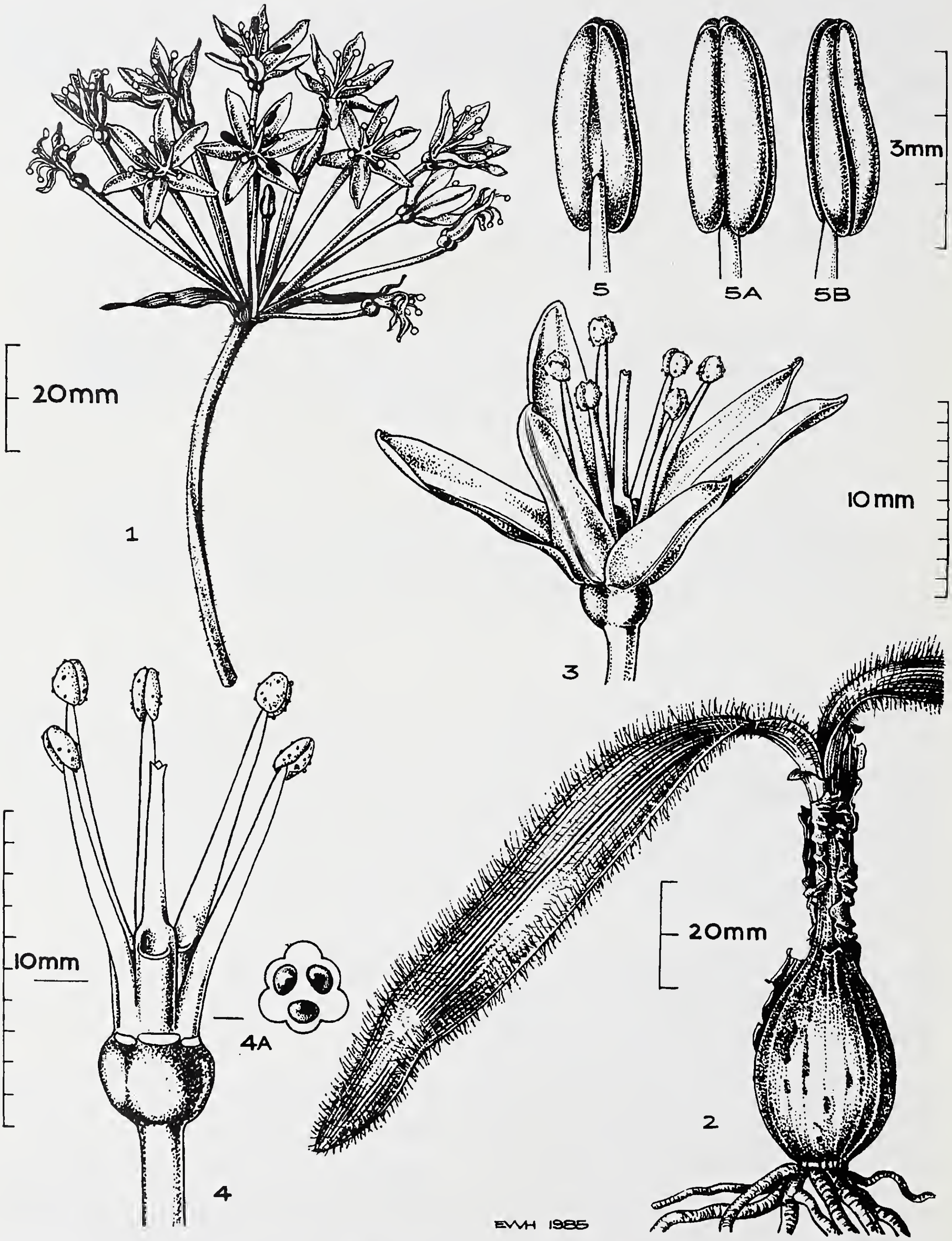

FIGURE 1.—*Strumaria aestivalis.* 1, inflorescence; 2, vegetative habit; 3, whole flower; 4, androecium and gynoecium with free portion of foremost stamen removed; 4A, transverse section through base of androecium and style showing nectar wells between inner filaments and style; 5, anther attachment, dorsal view; 5A, ventral view; 5B, lateral view. Drawn from *Perry 1991.*

lanceolate, 30–50 × 5–7 mm; bracteoles filiform, up to 20 mm long. *Flowers* 10–20, spreading, widely funnel-shaped, white, with a pale pink median dorsal band on each tepal, turning deeper pink with age, heavily scented; pedicels straight to upwardly curved, 40–55 mm long, pale greenish-pink. *Tepals* free to the base, spreading, oblong-lanceolate, 12–14 × 3–5 mm. *Stamens* equalling the tepals, spreading slightly from near the base; filaments separate, 7–10 mm long, adnate to the broadened style base for up to 4 mm; the inner face of the inner whorl free with only the lateral margins adnate to the broadly triquetrous style, forming 3 tubular nectar wells; anthers subcentrifixed, ± 3 mm long before opening, wine-red; pollen cream-coloured. *Ovary* with 1–2 ovules per locule. *Style* up to 17 mm long, broadly triquetrous in the proximal third, tapering and slender distally. *Seeds* fleshy, ovoid, 4–6 mm diam., green to reddish brown. *Chromosome number*: 2n = 20.

Diagnostic features: *Strumaria aestivalis* is remarkable in having three wide nectar wells formed by the fusion of the lateral margins of the inner filaments with the winged edges of the triquetrous style (Figure 1.4A). This specialisation is also well developed in the species of *Strumaria* with leaves arranged in a fan (*S. truncata* Jacq., *S. hardyana* D. & U. Müller-Doblies, *S. barbarae* Oberm. and *S. phonolithica* Dinter) and indicates parallel development in *S. aestivalis* and this group. *Strumaria aestivalis* is most closely related to *S. pubescens* with which it shares yellow-fleshed bulbs and broadly lorate, pubescent leaves. Yellow inner bulb tunics were previously reported as a restricted character (Müller-Doblies 1985) but the data given here indicate that it is more widespread.

Distribution and phenology: the northwestern foothills of the Langberg, northwest of Loeriesfontein, is the only known locality of *S. aestivalis* (Figure 2). The population is confined to the southeast-facing banks of a seasonal stream, where the bulbs are aggregated in the shade of rocks or low shrubs, amongst shale chips overlying heavy loam, at elevations of 950 m. This site which lies east of the main winter rainfall region where *Strumaria* is centred, is located within a zone where the probability of rain is greatest in March (Zucchini & Adamson 1984). *S. aestivalis* responds rapidly to scattered summer thundershowers and flowers during January and February.

CAPE.—3018 (Kamiesberg): Farm Langberg, NW of Loeriesfontein, (–DB), *Perry 1991* (K, MO, NBG, PRE); 20-1-1986, *Snijman 1006* (MO, NBG).

2. **S. perryae** *Snijman*, sp. nov., ex affinitate *S. pubescentis* W.F. Barker et *S. aestivalis* Snijman, ab utroque bulbi tunicis albidis et foliis anguste loratis differt. Figure 3.

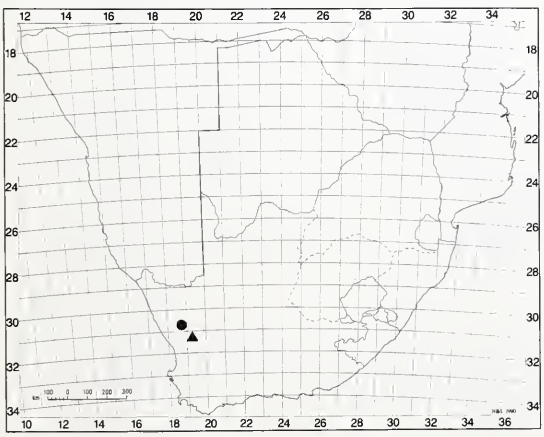

FIGURE 2.—The known geographical distribution of *Strumaria aestivalis*, ●; and *S. perryae*, ▲.

TYPE.—Cape Province, 3119 (Calvinia): (–AA), between Grasberg and Theunisdrift, NW of Nieuwoudtville, 15-5-1980, *Perry 997* (NBG, holo.; K, PRE, MO).

Bulb solitary, globose, 10–15 mm diam, with lightly fibrous light brown outer tunics, fleshy and whitish within; neck up to 45 mm long. *Leaves* absent at anthesis, 2, suberect to recurved, narrowly lorate to lanceolate, 50–150 (–250) × 2.5–5.0 mm, softly pubescent with hairs up to 2 mm long on both surfaces, flushed with red towards the base of the abaxial surface, subtended by a subterranean amplexicaul cataphyll and non-amplexicaul prophyll. *Inflorescence* somewhat clustered, 25–30 mm across; scape erect to flexuose, 50–165 (–240) mm long, ± 1 mm diam., reddish pink with a grey bloom, rarely pubescent, breaking off at the base in fruit; spathe valves linear-lanceolate, 15–20 × 1–2 mm; bracteoles filiform, up to 6 mm long. *Flowers* 3–11, more or less ascending, widely funnel-shaped, scentless; pale pink with a deeper pink median dorsal band on each tepal, turning deep pink with age; pedicels straight to upwardly curved, 20–30 (–60) mm long, pale green to reddish pink. *Tepals* shortly adnate to the filaments for up to 1 mm, otherwise free, the outer spreading more widely than the inner, oblong-lanceolate, 10–17 × 2.5–4.0 mm. *Stamens* suberect to slightly spreading, exserted beyond the tepals; filaments separate, up to 17 mm long, with the outer and inner whorls adnate to the style base for up to 2.5 mm and 3.5 mm respectively; anthers subcentrifixed, ± 3 mm long before opening, dark maroon; pollen cream-coloured. *Style* up to 19 mm long, equalling or slightly exceeding the stamens, slightly thickened and trigonous proximally, tapering gradually upwards; with nectar collecting in 3 droplets between the style and inner filaments; stigma shortly trifid. *Seeds* fleshy, ovoid, 2.0–2.5 mm diam., green to reddish brown. *Chromosome number*: 2n = 20.

Flowering time: May, but commencing in April when cultivated.

Diagnostic features: the long, lorate, pubescent leaves and somewhat funnel-shaped flowers of *S. perryae* are characteristics also found in *S. pubescens* and *S. aestivalis*, and indicate a close affinity with these species. The narrow leaves of *S. perryae* are diagnostic (at most 5 mm across). In contrast, *S. pubescens* and *S. aestivalis* have leaves more than 10 mm wide and the synapomorphy of yellow inner bulb tunics. The adnation of the filaments to the style is well developed and reaches a length of 3.5 mm. This feature is also conspicuous in specimens of *S. pubescens*, *S. watermeyeri* L. Bolus, as well as *S. aestivalis*. Unlike *S. aestivalis* the inner filaments of these species are closely adnate to the style and the three efferent canals, which conduct nectar from the septal nectary to the sinus between the inner filaments and style, are only microscopically visible.

Distribution and habitat: *S. perryae* is known from a single small population on the northern Bokkeveld escarpment between Grasberg and Theunisdrift, northwest of Nieuwoudtville (Figure 2). Plants grow in clay soil in association with low karroid shrubs.

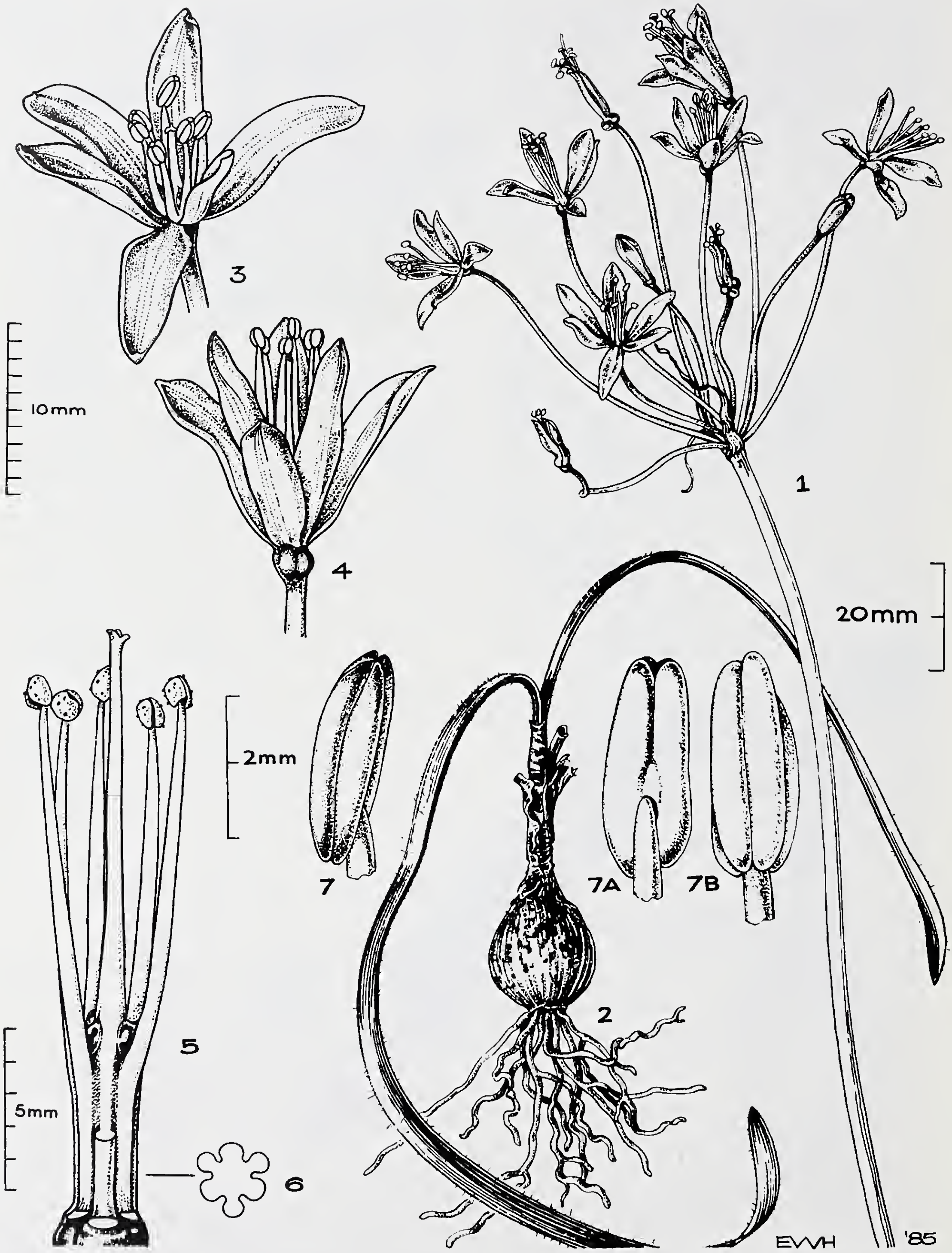

FIGURE 3.—*Strumaria perryae*. 1, inflorescence; 2, vegetative habit; 3 & 4, whole flowers; 5, androecium and gynoecium with free portion of foremost stamen removed and with nectar between the inner filaments and style; 6, transverse section through column formed by fusion of the stamens to the style; 7, anther attachment, lateral view; 7A, dorsal view; 7B, ventral view. Drawn from *Perry 997*.

Etymology: the epithet honours Miss Pauline Perry of the National Botanical Garden at Worcester, who discovered this species. She has also located several rare and poorly documented species of Strumariinae from Namaqualand.

CAPE.—3119 (Calvinia): between Grasberg and Theunisdrift, NW of Nieuwoudtville, (−AA), 15-5-1990, *Perry 997* (K, MO, NBG, PRE); ±7 km from Grasberg homestead towards Theunisdrift, (−AA), 8-5-1985, Snijman 867 (NBG).

3. **S. discifera** *Marloth ex Snijman*, sp. nov., a speciebus ad *Strumarium* sensu lato pertinentibus, bulbi tunicis interioribus albidis, foliis longis lanceolatis (ad 160 mm), pubescentia (certe in iuvenilibus), floribus stellaribus, tepalis canaliculatis, styli basi strumosa et strumae forma manifeste bulbiformi vel discoidea distincta.

TYPE.—Cape Province, 3118 (Vanrhynsdorp): (−DB), Bokkeveld Mountains, top of Koebee Pass, 18-4-1981, *Snijman 443* (NBG, holo.; K, PRE).

Bulbs solitary or forming large clumps, ovoid to subglobose, 10−20 mm diam., with outer tunics light brown and softly fibrous, fleshy and white or occasionally pale mauve within; neck (10−) 20−60 mm long. *Leaves* absent or incipient at anthesis, 2 or occasionally 3, suberect to prostrate, narrowly lanceolate, 20−160 × 3−10 mm, pubescence variable, with long soft hairs or short hairs covering both surfaces or the adaxial surface only, rarely glabrous, sometimes flushed with red towards the base of the abaxial surface, subtended by a subterranean amplexicaul cataphyll and non-amplexicaul prophyll. *Inflorescence* spreading, 25−130 mm across; scape somewhat flexuose, 50−140 mm long, ± 2 mm diam., green to reddish brown, glabrous or rarely pubescent, usually breaking off at ground level while fruiting; spathe valves linear-lanceolate, up to 30 × 3 mm; bracteoles filiform, up to 5 mm long. *Flowers* (2−) 5−16, spreading, stellate, glistening white, with an olive-green to pink median dorsal stripe on each tepal, scented or scentless; pedicels straight to upwardly curved, 20−75 mm long, concolorous with the scape. *Tepals* free to base, outspread, with the outer whorl often deflexed, oblong-lanceolate, 4−7 × 1.5−3.0 mm, channelled, sometimes abruptly conduplicate in the proximal third. *Stamens* equalling or slightly shorter than the tepals, spreading; filaments separate, adnate proximally to the swollen style, with the inner whorl usually attached slightly higher up than the outer; anthers subcentrifixed, approximately 2 mm long and wine-red before opening; pollen cream-coloured. *Ovary* with 1−3 ovules per locule. *Style* up to 7 mm long, equalling or shortly exceeding the stamens, variably dilated in the proximal half, either somewhat bulbiform or discoid with a prominent distal irregular rim, narrowly terete in the distal half, with nectar collecting in 3 droplets between the base and inner filaments; stigma shortly trifid. *Seeds* fleshy, ovoid 2.5−4.0 mm diam. green to reddish brown. *Chromosome number*: 2n = 20.

Flowering time: March to May.

Diagnostic features: in comparison to the group of closely allied pubescent-leaved species with white-fleshed bulbs and stellate flowers, *S. discifera* has consistently long, narrowly lanceolate leaves, distinctly channelled tepals and a conspicuous bulbiform to discoid swelling at the base of the style.

Distribution and variation: *Strumaria discifera* is distributed between Vanrhynsdorp and Nieuwoudtville eastwards to Calvinia and the Roggeveld escarpment in the northwestern Cape (Figure 5).

The species includes a polymorphic range of populations. From the dolerite ridges on the outskirts of Nieuwoudtville the bulbs are densely clump-forming, whereas other known populations comprise scattered solitary bulbs. The shape of the swelling at the base of the style is also variable. The clump-forming bulbs have a pronounced discoid stylar swelling with a frilly rim. This character state is fairly consistent within the population and is probably maintained through recurrent vegetative propagation. Collections east of Nieuwoudtville to the Hantamsberg and Bloukranz Pass near Calvinia also have disc-like swellings, but these are not as broad as those in the Nieuwoudtville populations and lack a prominent rim. Elsewhere in the distribution range the stylar swelling tends to be bulbiform in shape. Since the specimens from the clonal population on the dolerite koppies at Nieuwoudtville can be adequately diagnosed, these are described here as a new subspecies.

3a. **S. discifera** subsp. **discifera**. Figure 4.

Bulbs solitary. *Leaves* 20−120 × 4−10 mm, with 1−3 mm long, soft patent white hairs, occasionally both surfaces glabrous but then juveniles pubescent. *Scape* glabrous. *Tepals* 5−6 × 1.5−3.0 mm, channelled evenly throughout. *Style* smoothly bulbiform or irregularly thickened and longitudinally ridged in the proximal quarter.

Distribution and habitat: the known distribution extends from near Vanrhynsdorp, eastwards onto the Bokkeveld escarpment, across the high-lying plateau to Calvinia, then southwards along the edge of the Roggeveld escarpment to near Middelpos (Figure 5). Occupying gentle slopes and depressions, the taxon inhabits heavy loamy soils, most commonly derived from Nama and Ecca shales. The bulbs often grow in association with renosterbos (*Elytropappus rhinocerotis* (L.f.) Less.).

CAPE.—3019 (Loeriesfontein): Kafferdam, about 6 km NW of Loeriesfontein on road to Kubiskouw Mountain, (−CD), *Lavranos 27602* (NBG). 3118 (Vanrhynsdorp): N banks of Wiedourivier, near bridge between Klawer and Vanrhynsdorp, (−DA), *Snijman 261* (K, MO, NBG, PRE); top of Koebee Pass, Bokkeveld Mountains, (−DB), 26-4-1988, *Snijman 1172* (NBG, PRE), *Snijman 443* (K, NBG, PRE). 3119 (Calvinia): Glenridge, (−AC), *Barker 4672* (NBG); Glen Lyon, (−AC), 3-4-1982, *Perry 1824* (K, MO, NBG, PRE); *Mauve & Oliver sub G.N. 19699* (PRE); 5 miles E of Nieuwoudtville towards Calvinia, (−AC), 18-4-1969, *Barker 10613* (NBG); 11 km E of Nieuwoudtville towards Calvinia, (−AC), *Perry 1014* (MO, NBG, PRE); Akkerdam, lower slopes of Hantam Mountains, (−BD), *Barker 9344* (NBG); Bloukranz Pass, (−DA/DB), *Bayer 1853* (NBG); Farm Blomfontein, Roggeveld escarpment, (−DD), 10-5-1985, *Snijman 876* (NBG).

3b. **S. discifera** subsp. **bulbifera** *Snijman*, subsp. nov., a subspecie typica bulbo prolifero, styli basi strumosa, strumae forma discoidea et margine irregulari prominenti supra strumam distincta.

TYPE.—Cape Province, 3119 (Calvinia); (−AC), Nieuwoudtville Wildflower Reserve, 19-4-1983, *Perry & Snijman 2042* (NBG, holo.; K, MO, PRE, S). Figure 6.

Bulb producing bulblets and forming dense clumps. *Leaves* 6.5−150.0 × 3−10 mm, both surfaces covered with

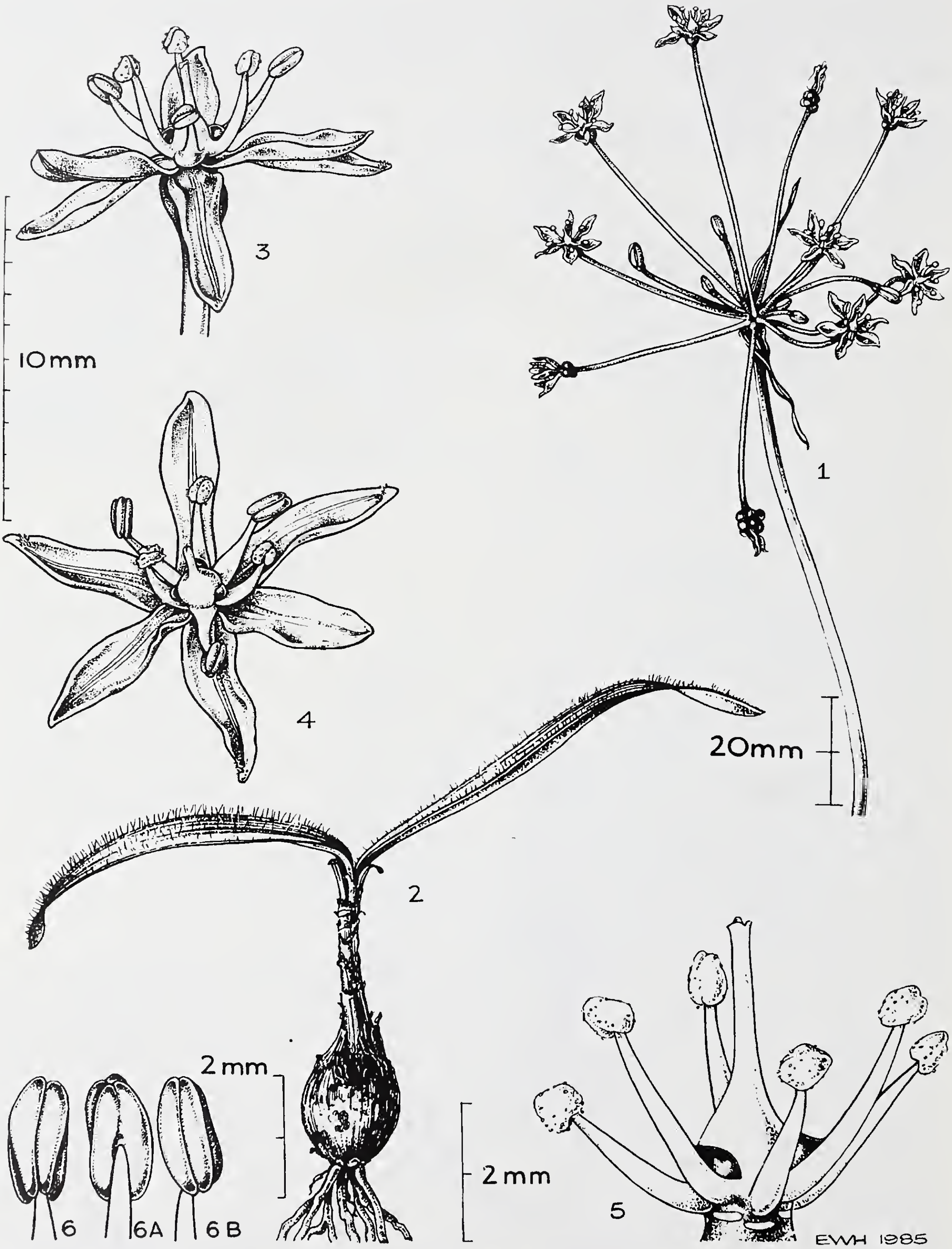

FIGURE 4.—*Strumaria discifera* subsp. *discifera*. 1, inflorescence; 2, vegetative habit; 3 & 4, whole flowers; 5, androecium and style with nectar droplets between the inner filaments and style; 6, anther attachment, ventral view; 6A, dorsal view; 6B, lateral view. Drawn from *Snijman 261*.

2 mm long, white, patent hairs; adaxial surface flushed with red proximally. *Scape* minutely pubescent or glabrous. *Tepals* 5–7 × 2–3 mm, abruptly conduplicate at a point almost a third from the base, otherwise channelled; outer whorl slightly deflexed. *Style* discoid proximally, with a prominent irregular rim on the disc distally, abruptly narrowed into a slender column above.

Distribution and habitat: subsp. *bulbifera* inhabits slopes and hollows of low exposed dolerite ridges on the Bokke-

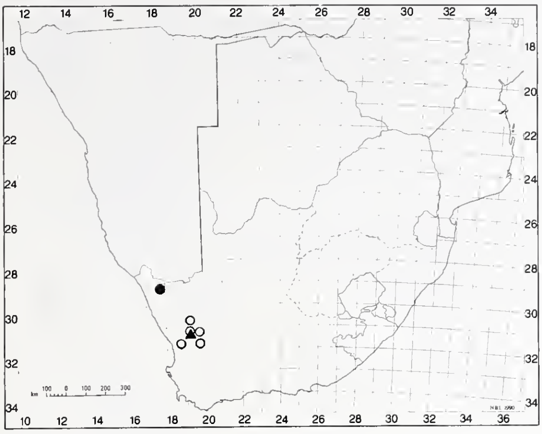

FIGURE 5.—The known geographical distribution of *Strumaria discifera* subsp. *discifera*, ○; *S. discifera* subsp. *bulbifera*, ▲; and *S. villosa*, ●.

veld escarpment near Nieuwoudtville (Figure 5). The densely aggregated bulbs grow in deep, red loamy soils, in association with open low, succulent shrubland.

CAPE.—3119 (Calvinia): Meulsteen Vley, (—AC), 2-5-1927, *Watermeyer in Herb. Afr. Bol. 18648* (BOL); top of Vanrhyn's Pass, (—AC), 30-4-1946, *Smith 6490* (NBG); Farm Glen Lyon, (—AC), 8-5-1985, *Snijman 863* (NBG, PRE); Nieuwoudtville Wildflower Reserve, (—AC), 19-4-1983, *Perry & Snijman 2042* (K, MO, NBG, PRE, S).

4. **S. villosa** *Snijman*, sp. nov., a speciebus ad *Strumariam* sensu lato pertinentibus, bulbi tunicis interioribus luteis, foliis glaucis, pubescentia in pagina adaxiali folii, floribus stellaribus, styli basi amplificata distincta. Figure 7.

TYPE.—Cape Province, 2917 (Springbok): (—BA), Richtersveld, 29° 10.05′S, 17° 41.49′E, E of Kosies, 3200 ft, 29-3-1981, *Van Berkel 311* (NBG, holo.; K, PRE).

Bulb solitary, subglobose, 15—25 mm diam., with light brown lightly fibrous outer tunics, fleshy and yellowish within; neck up to 35 mm. *Leaves* absent at anthesis, 2 prostrate, narrowly elliptical to lorate, 30—85 × 10—15 mm; adaxial surface glaucous, covered with 2.5 mm long, soft white, patent hairs; abaxial surface glabrous, shiny green, subtended by a subterranean amplexicaul cataphyll and non-amplexicaul prophyll. *Inflorescence* spreading, 30—100 mm across; scape slightly flexuose, 60—140 × 2—3 mm, pale green to pink with a grey bloom, breaking loose at the base in fruit; spathe valves linear-lanceolate, 15—20 × 4 mm; bracteoles filiform, up to 5 mm long. *Flowers* 8—14, spreading, stellate, pure white or white to pale pink with a pale pink median dorsal stripe on each tepal, scentless; pedicels straight to upwardly curved, 35—80 mm long, concolorous with the scape. *Tepals* free to the base, outspread to slightly deflexed, oblong-lanceolate, 6.5—8.5 × 2—3 mm, distinctly channelled with slightly undulate margins proximally. *Stamens* equalling or slightly shorter than the tepals, spreading; filaments separate, adnate to the broadened style base, with the inner whorl attached higher up than the outer, broad but not bulbous basally, tapering slightly upwards; anthers subcentrifixed, 1.5 mm long and wine-red before dehiscing; pollen whitish. *Ovary* with 1—4 ovules per locule. *Style* up to 5 mm long, more or less equalling the stamens, tapering smoothly upwards from a broad obscurely conoidal base, with nectar collecting in 3 droplets between the style base and inner filaments; stigma shortly trifid. *Seeds* fleshy, ovoid, approximately 2 mm diam. green to reddish brown. *Chromosome number*: 2n = 20 + 2—3B.

Flowering period extends from March to April.

Diagnostic features: the leaves of *S. villosa* are softly villous on the adaxial surface and are characteristically glaucous. Unlike other pubescent-leaved species of the Strumariinae with white, stellate flowers and filaments adnate to the style, *S. villosa* is specialized in having yellow inner bulb tunics.

Distribution and habitat: this rare species is known from only one locality in the Richtersveld, near Kosies, (Figure 5). Locally abundant on low hills, the species is confined to exposed, east-facing slopes amongst quartz pebbles which overlie weathered granite soil.

CAPE.—2917 (Springbok): 29° 10.05′S, 17° 41.49′E of Kosies, (—BA), *Van Berkel 156* (NBG); 29-3-1981, *Van Berkel 311* (K, NBG, PRE); *Perry 1544* (K, MO, NBG, PRE, S).

5. **H. speciosa** *Snijman*, sp. nov., quoad tubum brevissimum perigonii et tepala plana ad *Hesseam pilosulam* D. & U. Müller-Doblies et *H. incanam* Snijman accedit, sed ab ambobus foliis glabris et staminibus longioribus (aequantibus vel superantibus tepala) satis differt. Figure 8.

TYPE.—Namibia, 2818 (Warmbad): (—CA), Warmbad District, Farm Witpütz, 15-5-1963, *Giess, Volk & B. Bleissner 6960* (WIND, holo.; PRE).

Bulb solitary, deep-seated, subglobose, 25—60 mm diam., covered with several layers of cream-coloured cottony fibrous tunics, extended into a stout neck 100—170 mm long. *Leaves* absent at anthesis, 2, recurved, lorate, up to 120 × 4—6 mm, plane, glabrous, dark green and flushed with red towards the base; amplexicaul cataphyll remaining subterranean; prophyll unknown. *Inflorescence* dense, hemispherical to spherical, 70—120 mm across; scape erect to somewhat flexuose, 60—160 × 3—5 mm, initially green, breaking off at the base in fruit; spathe valves linear-lanceolate, 20—40 × 3—7 mm; bracteoles filiform, up to 25 mm long. *Flowers* (20—) 30—65, spreading, stellate, white to delicate pink with deep pink or greenish median stripes on the undersurface, ageing to light brown, with a heavy coconut-like scent; pedicels straight, 20—50 mm long, becoming straw-coloured. *Tepals* almost free to the base or very shortly adnate to the staminal tube for up to 0.25 mm, otherwise outspread, oblong-lanceolate, 8—15 × 2—4 mm, with plane edges. *Stamens* equalling or up to 2 mm longer than the tepals, becoming outspread; filaments connate proximally into a tube protruding from the perigone throat by (1.0—) 1.5—4.0 mm, subulate above, occasionally shortly toothed in the axils between adjacent filaments; anthers centrifixed, 3 mm long and dark wine-red before opening; pollen cream-coloured. *Style* up to 15 mm long, narrow throughout, with nectar collecting in a well around the base; stigma shortly trifid. *Seeds* not known. *Chromosome number*: 2n = 22.

Flowering time: from late March into May.

Diagnostic features are the deep-seated bulb with a long neck (up to 170 mm); the somewhat spherical inflores-

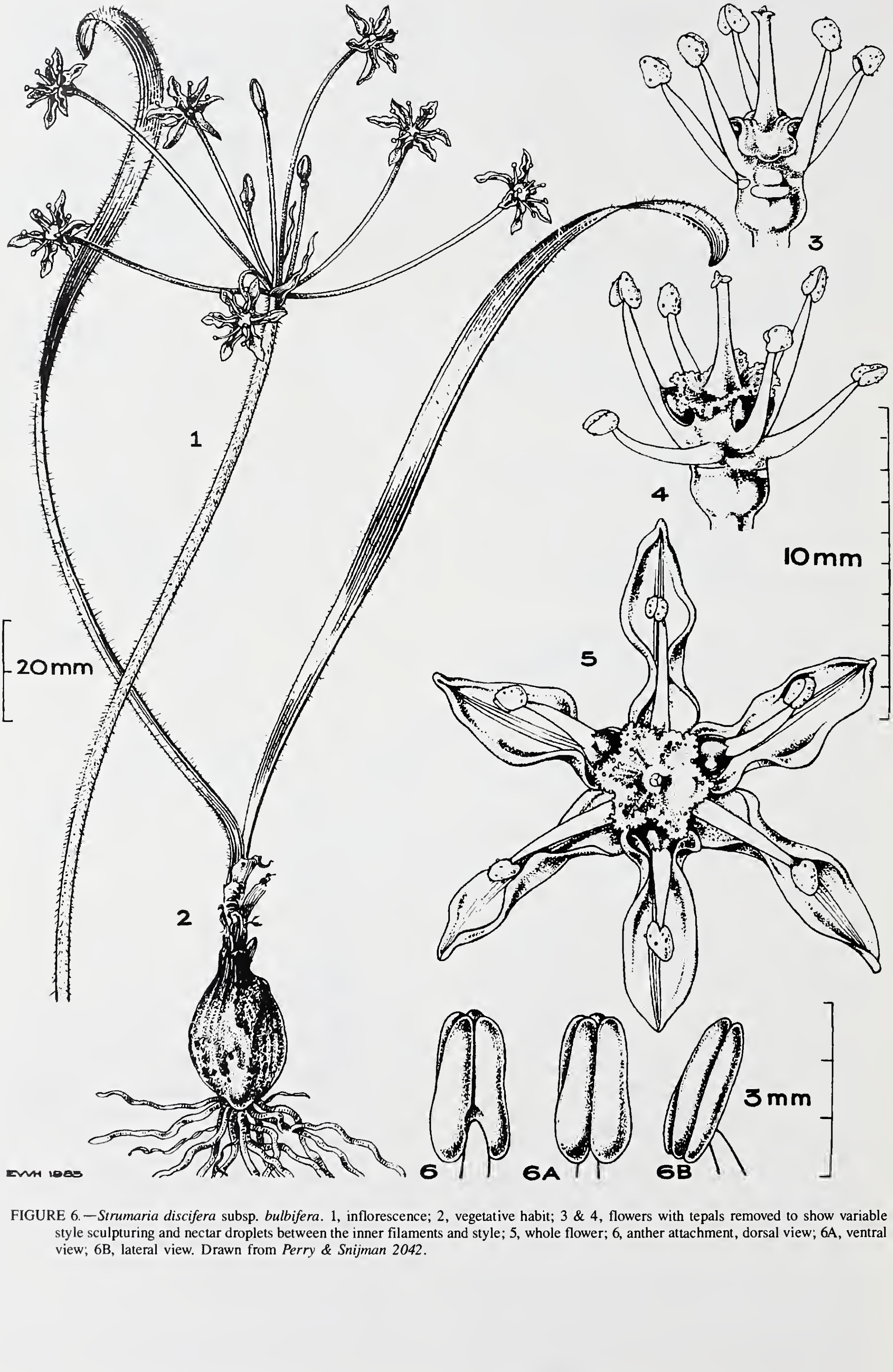

FIGURE 6.—*Strumaria discifera* subsp. *bulbifera*. 1, inflorescence; 2, vegetative habit; 3 & 4, flowers with tepals removed to show variable style sculpturing and nectar droplets between the inner filaments and style; 5, whole flower; 6, anther attachment, dorsal view; 6A, ventral view; 6B, lateral view. Drawn from *Perry & Snijman 2042*.

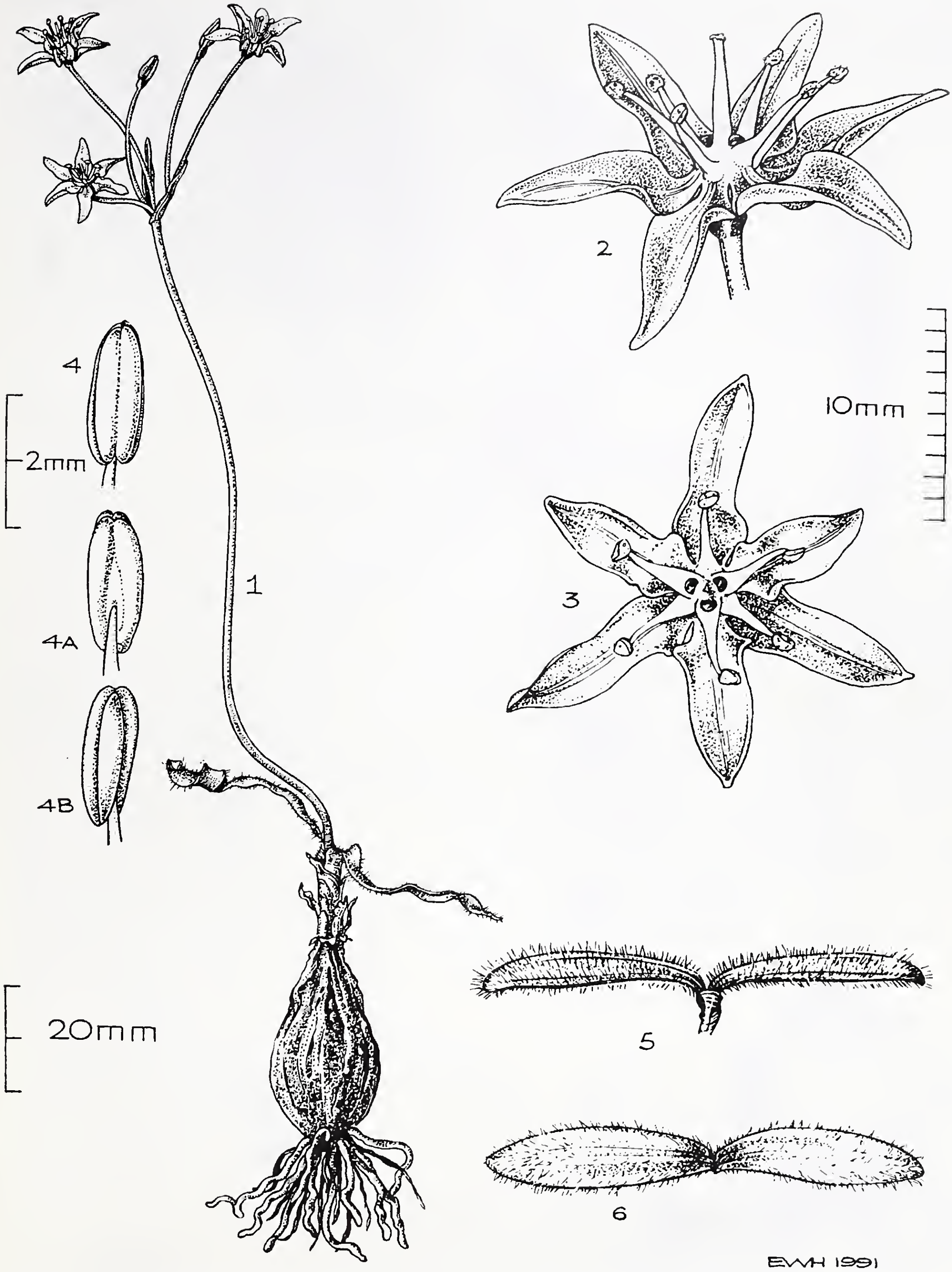

FIGURE 7.—*Strumaria villosa*. 1, plant with inflorescence; 2 & 3, flowers indicating the attachment of the filaments to the style base and nectar droplets between the inner filaments and style; 4, anther attachment, dorsal view; 4A, ventral view; 4B, lateral view; 5 & 6, leaves. Drawn from *Van Berkel 156*.

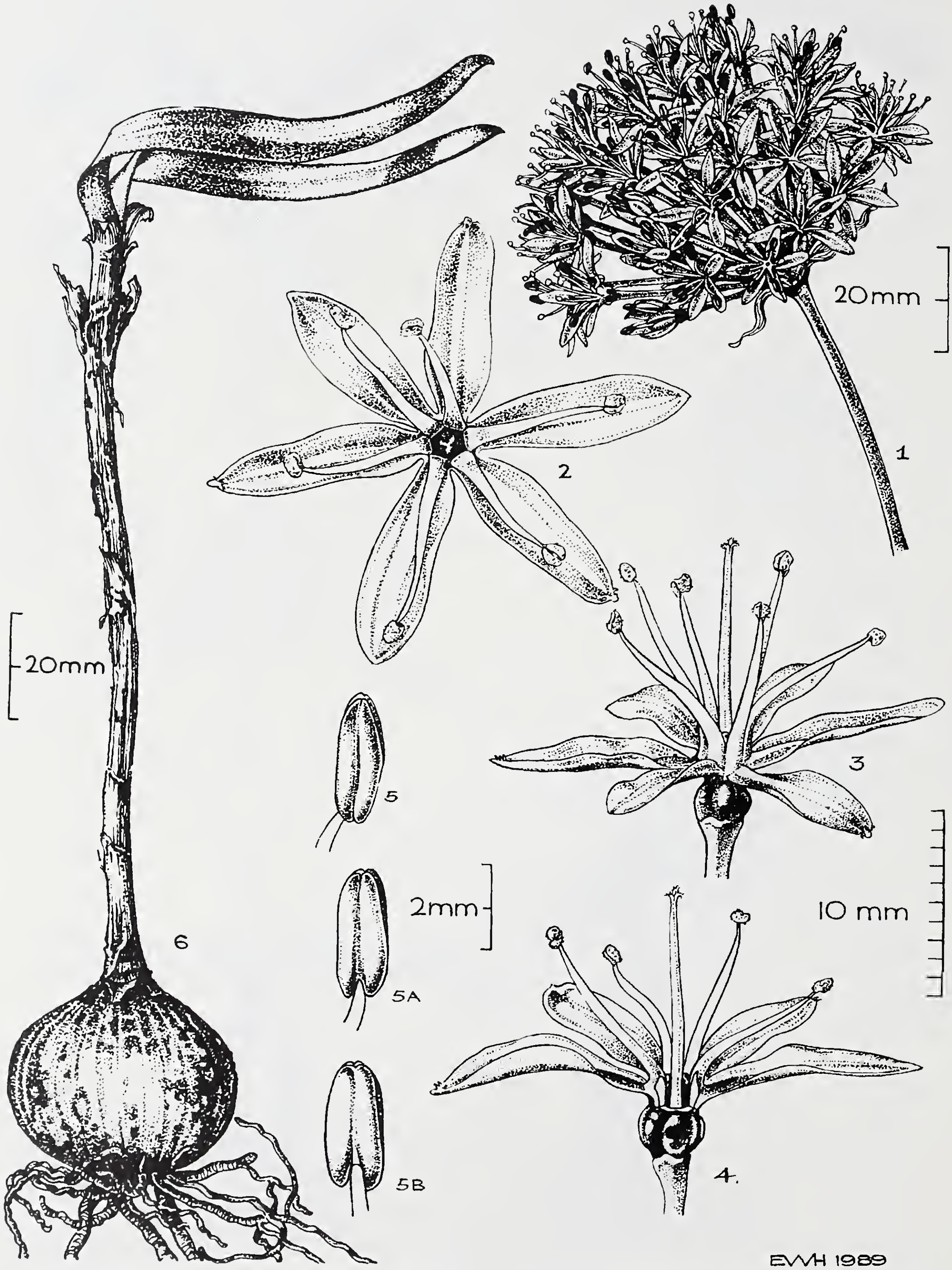

FIGURE 8.—*Hessea speciosa*. 1, inflorescence; 2 & 3, whole flowers; 4, partial section of flower; 5, anther attachment, lateral view; 5A, ventral view; 5B, dorsal view; 6, vegetative habit. Drawn from *Snijman 1163*.

cence; and the very short perigone tube (0.25 mm or less). In these respects *H. speciosa* is similar to the shortly pubescent-leaved species, *H. pilosula* D. & U. Müller-Doblies and *H. incana* Snijman, with which it also shares plane tepals. However, the glabrous leaves and the relative length of the stamens to the tepals distinguish it from these species. The stamens equal to or up to 2 mm longer than the tepals in *H. speciosa*, whereas they are distinctly shorter than the tepals (by 3 mm or more) in *H. pilosula* and *H. incana*. The inflorescence of *H. speciosa* may sometimes be confused with flowering material of *H. breviflora* Herb. from Namaqualand, but unlike this species the bulbs are without a conspicuous, exserted, red cataphyll which sheathes the foliage leaves.

Distribution and habitat: *Hessea speciosa* is recorded from red sand dunes and flats of friable loam, associated with the extensive drainage system of seasonal rivers from Warmbad in southern Namibia to Fraserburg in the central Cape. The associated vegetation is predominantly grassveld (Figure 9).

Variation: often the northerly populations have a distinct staminal tube (1.5–3.5 mm long), whereas specimens from the south of the distribution range have only a shortly developed staminal tube (less than 1.5 mm). Both white and pale pink flower forms occur, as well as the occasional novelty of small teeth in the axils between adjoining filaments.

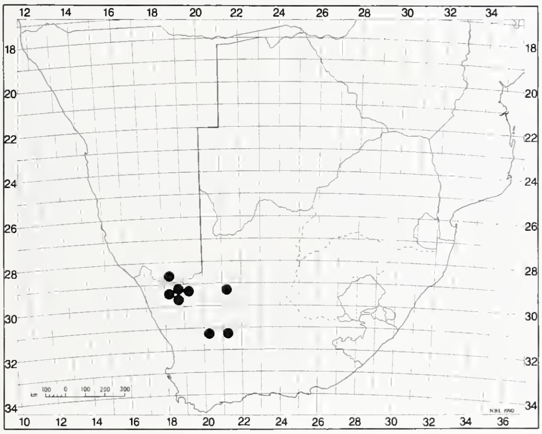

FIGURE 9.— The known geographical distribution of *Hessea speciosa*.

NAMIBIA.—2818 (Warmbad) Warmbad District, Farm Witpütz, (–CA), 15-5-1963, *Giess, Volk & B. Bleissner 6960* (PRE, WIND); 15-5-1963, *S. Bleissner 268* (PRE).

CAPE.—2918 (Gamoep): Farm Eendop, SW of Klipvlei, (–AC), 1-5-1981, *Van Berkel 331* (NBG); Aggenys Mine, (–BB), 23-5-1989, *S. Dean 655* (NBG); Banke, Pofadder, (–DB), 3-5-1988, *S. Dean s.n.* (NBG). 2919 (Pofadder): Farm Kykgate, along road between Springbok and Pofadder, (–AC), 13-5-1969, *Van Breda 4147* (PRE). 2921 (Kenhardt): Kenhardt, (–AC), 9-5-1927, *Long sub NBG 947/27* (BOL); 14-5-1936, *Martin sub NBG 1188/36* (BOL). 3120 (Williston): 40 miles N of Calvinia, (–AA/AB), 30-3-1953, *Hall 684* (NBG); 36 km N of Downes towards Brandvlei, (–AC), 3-4-1988, *Snijman 1163* (NBG, PRE). 3121 (Fraserburg): 49 miles from Fraserburg towards Williston, (–AC), *Smith 6491* (NBG).

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Three new species of *Diascia* (Scrophulariaceae) from the western Cape

K. E. STEINER*

Keywords: breeding system, *Diascia*, new species, Scrophulariaceae

ABSTRACT

Three annual *Diascia* species are described from the western Cape. Two species, *D.* **maculata** K.E. Steiner and *D.* **humilis** K.E. Steiner have small flowers and are closely related. *D.* **maculata** is characterized by a slightly gibbous corolla with no spurs or sacs, erect stamens, and a distinct patch of oil-secreting trichomes in the tube at the base of each upper and lateral corolla lobe. *D.* **humilis** is characterized by a bisaccate corolla, forward projecting stamens and oil-secreting trichomes localized in corolla sacs. The third new species, *D.* **hexensis** K.E. Steiner, is most similar to *D. sacculata* Benth., but it differs from that species by its larger flowers and much longer spurs which curve downward instead of upward.

UITTREKSEL

Drie eenjarige *Diascia*-spesies van die Wes-Kaap word beskryf. Twee spesies, *D.* **maculata** K.E. Steiner en *D.* **humilis** K.E. Steiner het klein blomme en is na verwant. *D.* **maculata** word gekenmerk deur die effens bulterige blomkroon sonder spore of sakkies, die regop meeldrade, en 'n duidelike gebied met olie-afskeidende trigome in die kroonbuis aan die basis van elke boonste en laterale blomkroonlob. *D.* **humilis** word gekenmerk deur die tweesakkige blomkroon, die meeldrade wat na vore gerig is, en die olie-afskeidende trigome wat tot die sakkies van die blomkroon beperk is. Die derde nuwe spesies, *D.* **hexensis** K.E. Steiner, kom in baie opsigte met *D. sacculata* Benth. ooreen, maar verskil daarvan in die groter blomme en veel langer spore wat afwaarts in stede van opwaarts krul.

INTRODUCTION

Diascia section *Diascia* comprises approximately 41 species of annuals centred in the western Cape of South Africa. This group is currently under revision and has been found to contain many undescribed species. Three new species are described below.

D. maculata *K.E. Steiner*, sp. nov., *D. humili* K.E. Steiner proxima, sed differt corolla gibbosa (nonbisaccata), staminibus porrectis (non erectis), trichomatibus oleum secernentibus in tubo corollae basi loborum superorum lateraliumque corollae (non in sacculis corollae).

TYPE.—Cape, 3119 (Calvinia); 300 m north of Nieuwoudtville Caravan Park, (–AC), 740 m, 21-viii-1990, *Steiner 2165* (NBG, holo.; K, MO, PRE, US).

Annual herb, glabrous, simple or branching from the base. *Stems* up to 220 mm long, erect or decumbent, tetragonal in cross section, up to 1.5 mm on a side. *Basal leaves* few to many, rosulate or clustered, simple, petiolate, spreading or ascending, lamina 4–23 mm long, ovate to elliptic, apex rounded to acute, base attenuate, margins nearly entire to irregularly lobed or divided, divisions up to ± 3 mm long, oblong-ovate to triangular, entire, acute to acuminate; petioles up to ± 21 mm; stem leaves smaller, becoming reduced upwards, alternate, opposite or verticillate. *Flowers* axillary, one or two flowers open per stem, nodding in bud, pedicels 22–41 mm long, ascending, broadened and dorsiventrally flattened specially where attached to flower, recurving in fruit. *Calyx* lobes five, ± equal, ± 2.0–2.5 × 0.8–1.0 mm, spreading, or the lateral two slightly reflexed, lanceolate, acuminate, margins white ciliate. *Corolla* bilabiate, limb ± 7.4–10.5 × 8.6–11.0 mm; upper lobes ± 2.2–3.0 × 2.0–2.8 mm, oblong-ovate, rounded; lateral lobes ± 2.7–3.6 × 2.3–3.4 mm, ovate, rounded, bases oblique; lower lobe ± 3.0–3.9 × 2.9–5.0 mm, obovate, rounded to emarginate, upper lobes yellowish pink distally, bases purplish red with red veins or uniformly reddish purple, other lobes similar in colour but lacking veins, all lobes with dark purple-tipped glandular trichomes, especially on inner surface near the base; tube ± 1.0–2.0 mm, reddish purple with yellow spots below upper and lateral lobes, yellow patch below each upper lobe consisting of a single spot or 3 or 4 separate or partially coalesced spots, patch below each lateral lobe a single ± 1 mm long elliptical patch corresponding to a gibbous portion of the tube, yellow patches below lateral and upper lobes usually separated by a narrow strip of reddish purple tissue, but sometimes consisting of a single spot spanning the sinus between upper and lateral lobes; gibbous portion of tube with two patches of oil-secreting trichomes, a ± 1 mm long elliptical patch below each lateral lobe and a ± 0.3 mm patch at base of each upper corolla lobe near the sinus with the lateral lobe; spurs or sacs absent; central portion of tube turned outward to form a boss bearing the stamens, boss ± 1.2–1.5 mm high, connected to the upper lip by a septum. *Stamens* four, projecting forwards, anticous filaments (appearing posticous due to twisting of the bases) ± 1.5–1.7 mm long, curved and bearing a few scattered trichomes, posticous filaments (appearing anticous) ± 1.2–1.5 mm long, ± straight, widened and bilobed or simply strongly bent backward just below the anthers, anthers ± 0.2–0.5 mm, strongly cohering, yellow, attached to posticous lobes of filaments if bilobed, pollen usually orange. *Ovary* ± 1.2 × 0.7 mm, ovate in outline with purple markings on upper two thirds to one half, style ± 0.7–0.8 mm long, straight, stigma subcapitate, surrounded by anthers, ovules ± 50–55. *Capsule* ± 4.7–6.0 × 2.7–3.0 mm, falciform-

* Compton Herbarium, National Botanical Institute, Private Bag X7, Claremont 7735.
MS. received: 1991-07-09.

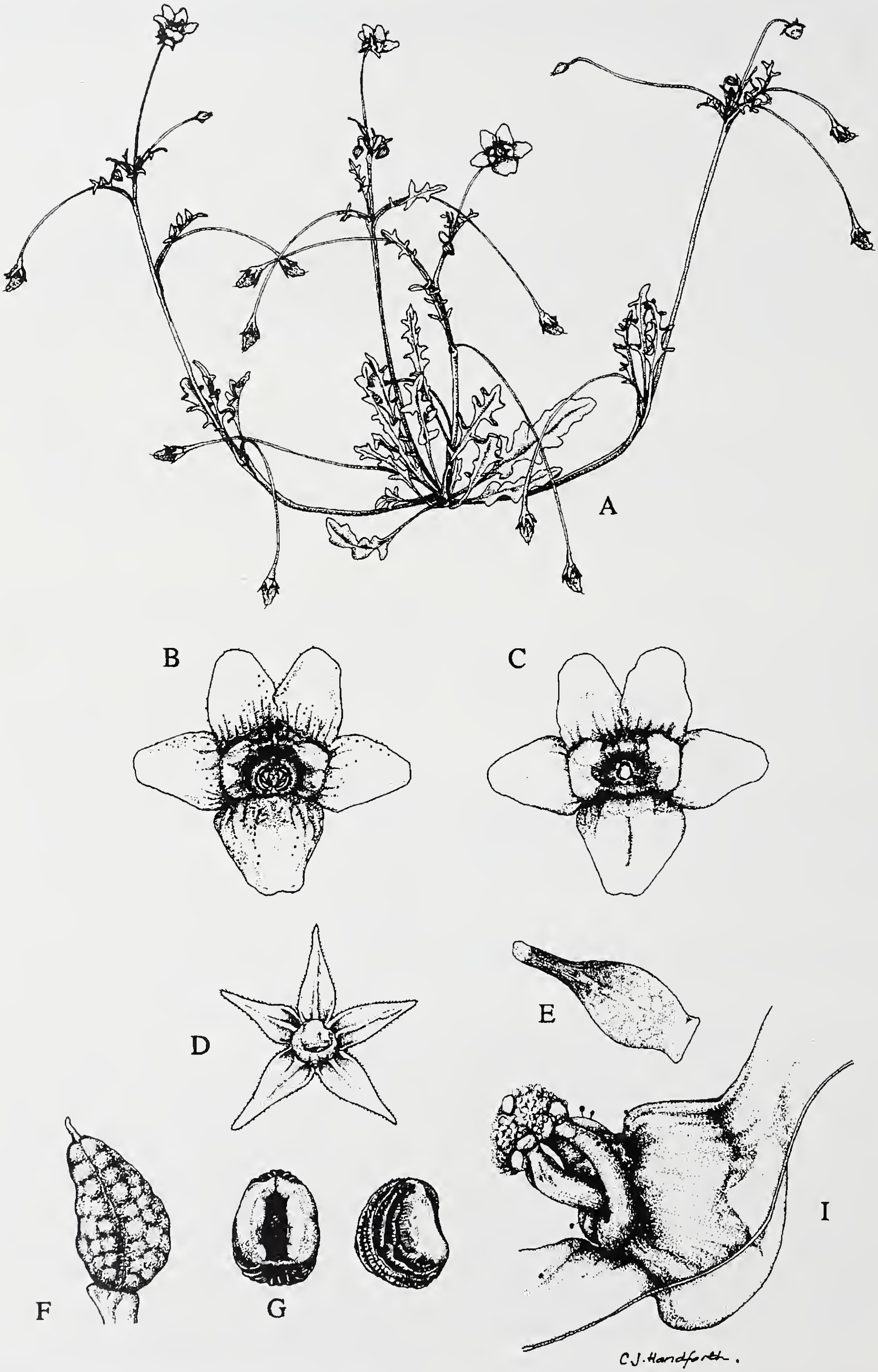

FIGURE 1.—*Diascia maculata, Steiner 21651.4*: A, habit, × 1; B, flower, front view, × 4.2; C, flower, rear view, × 4.2; D, calyx, × 7.8; E, gynoecium, × 16.2; F, capsule, × 6; G, seed, ventral view, × 25; H, seed, side view, × 25; I, androecium, × 16.2.

ovate in outline, exceeding calyx at maturity; seeds ± 0.65–0.85 mm long, dorsal surface ridged, ventral surface with seed coat extended to form a cupule with an oblong elliptical opening. Figure 1.

Flowering time: August–October.

Diagnostic features: *Diascia maculata* is characterized by a slightly gibbous corolla with no spurs or sacs, stamens that project forwards, and a distinct patch of oil-secreting trichomes (cf. Vogel 1974) in the tube at the base of each upper and lateral corolla lobe. In most populations, there is a yellow spot corresponding to the trichome patches. The pair of spots below one upper and one lateral lobe can be partially confluent or separated by a small strip of reddish purple tissue. The spotting pattern at one locality, the Matroosberg, is slightly different. There, the single elliptical yellow spot below each lobe characteristic of other populations is broken up into several smaller vertically oriented narrowly elliptic spots that are either distinct or only partially confluent. The specific epithet refers to the yellow spotting pattern of the corolla tube.

Diascia maculata is most closely related to *D. humilis* which has flowers of a similar size and colour. These two species also have very similar capsules, seeds, and pollen colour and can occur sympatrically on recently (less than one year old) burned fynbos (Farm Welkom) and renosterveld (Farm Matroosberg). *D. maculata* is distinguished most easily from *D. humilis* by the position of the stamens in relation to the upper corolla lobes, the presence of four distinct oil-secreting trichome patches and the absence of corolla sacs or spurs. The corolla tube of *D. maculata* is very similar to that of *D. gracilis* Schltr., since both species are somewhat gibbous; however, in *D. gracilis* the stamens are erect rather than projecting forward and the long linear capsules are usually more than four times as long as wide, not falciform-ovate and only ± twice as long as wide.

Distribution and habitat: *D. maculata* ranges from the Hex River Mountains in the southwestern Cape north to the Kamiesberg in Namaqualand (Figure 2). It ranges in elevation from 640 to 1 130 m. Despite its broad geographical range, *D. maculata* is known from relatively few collections. This may be due to overall rarity, a dependence on first year burns or small, easily overlooked, flowers.

Breeding system: *D. maculata* is autogamous; however, because it secretes floral oil, it may be visited and cross-pollinated, at least occasionally, by small short-legged oil-collecting *Rediviva* bees (Melittidae) (cf. Steiner & Whitehead 1988, 1990, 1991; Whitehead & Steiner 1985).

CAPE.— 3018 (Kamiesberg): Farm Welkom, 6.4 km south of junction with Garies–Platbakkies Road, (–AC), 1 130 m, 30-ix-1988, *Steiner 1852* (NBG). 3119 (Calvinia): old Nieuwoudtville road, 3.5 km west of main road in Nieuwoudtville, (–AC), ± 820 m, 10-ix-1986, *Steiner 1359* (NBG); Farm Lokenburg, ± 7.1 km southwest of Oorlogskloof road, (–CA), ± 640 m, 25-ix-1986, *Steiner 1393* (NBG). 3319 (Worcester): Farm Matroosberg, Hex River Pass, ± 5 km east of turnoff to De Doorns on the National Road (N1), (–BD), ± 710 m, 3-x-1989, *Steiner 2037* (NBG).

D. humilis *K.E. Steiner*, sp. nov., *D. maculatae* K.E. Steiner proxima, sed differt corolla bisaccata (non gibbosa), staminibus erectis (non porrectis), trichomatibus oleum secernentibus in sacculis corollae (non in tubo corollae basi loborum superorum lateraliumque corollae).

TYPE.—Cape, 3119 (Calvinia); Farm Koerdemoefontein, 5.9 km east of Oorlogskloof road on road to Clanwilliam (R364), (–CD), ± 720 m, 15-ix-1989, *Steiner 2005* (NBG, holo.; E, K, MO, PRE).

Annual herb, glabrous, simple or branching from the base. *Stems* up to 250 mm long, erect or decumbent, tetragonal in cross-section, up to 1.5 mm on a side. *Basal leaves* few to many, rosulate or crowded, simple, petiolate, spreading or ascending; lamina 4–41 mm long, ovate to elliptic, apex rounded to acute, base attenuate, margins nearly entire to irregularly lobed or divided; divisions up to ± 3 mm long, oblong-ovate to narrowly triangular, entire, acute; petioles up to ± 12 mm; stem leaves smaller, becoming reduced and more dissected upwards, 3-verticillate. *Flowers* axillary, one or two open per stem, nodding in bud, pedicels 16.0–20.5 mm long, ascending, broadened and dorsiventrally flattened especially where attached to the flower, recurving, but with the capsule turned up slightly, in fruit. *Calyx* lobes five, ± equal, ± 1.8–2.8 × 0.7–1.0 mm, spreading, lanceolate, acuminate, margins white ciliate. *Corolla* bilabiate, limb 6.2–7.6 × 7.0–8.6 mm; upper lobes ± 1.4–2.5 × 1.7–2.0 mm, falciform-oblong to oblong-ovate, rounded; lateral lobes ± 2.3–3.0 × 1.9–2.4 mm, broadly ovate, rounded, bases oblique; lower lobe 2.4–3.0 × 2.5–3.1 mm, obovate, rounded to emarginate, upper lobes yellowish pink or reddish purple, with red veins at the base, other lobes similar in colour but lacking veins, all lobes with sessile or semi-sessile dark purple glandular trichomes, especially on inner surface near the base; tube ± 1.0–1.5 mm, distended at base of each lateral lobe into a shallow yellow sac, ± 1.8 mm long, sacs containing yellow oil-secreting trichomes, especially near the tips; central portion of tube turned out to form a boss bearing the stamens, boss ± 1.2–1.5 on anticous side and 0.2–0.3 mm on posticous side, reddish purple in front and back and yellow on sides, connected to the upper lip by a septum. *Stamens* four, erect, anticous filaments (appearing posticous due to twisting of the base), touching the upper corolla lip, ± 2.0 mm long, reddish purple, falciform, glabrous or with a few scattered purple clavate trichomes, posticous filaments (appearing anticous) ± 1.5–1.6 mm, reddish purple, ± straight, except just

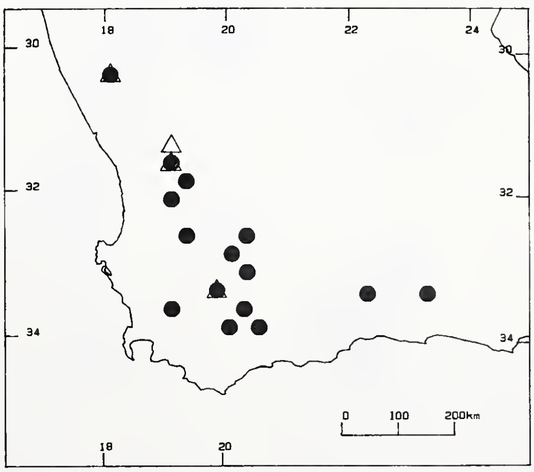

FIGURE 2.—Known geographic distribution of *Diascia maculata*, △; and *D. humilis*, ●, in South Africa.

below the anther where there is a sharp nearly 90° bend and broadening of the filament sometimes with a sterile outgrowth in the opposite direction, bend or outgrowth with purple clavate trichomes; anthers ± 0.20–0.30 mm, strongly cohering, pale pink or whitish, pollen usually orange. *Ovary* ± 1.3–1.4 × 0.6–1.0 mm, ovate in outline, sometimes with purple markings on upper half, style ± 0.70–0.75 mm long, straight, stigma surrounded by anthers, ovules ± 40–60. *Capsule* ± 5.0–6.5 × 2.6–3.0 mm, falciform-ovate in outline, exceeding calyx at maturity; seeds ± 0.65–0.90 mm long, falciform in outline, dorsal surface ridged, ventral surface with seed coat extended to form a cupule with an oblong-elliptical opening. Figure 3.

Flowering time: August–October.

Diagnostic features: *D. humilis* is characterized by small, usually yellowish pink flowers, its erect stamens, orange to red-orange pollen and small yellow sacs. It is most similar to *D. maculata* with which it can often be

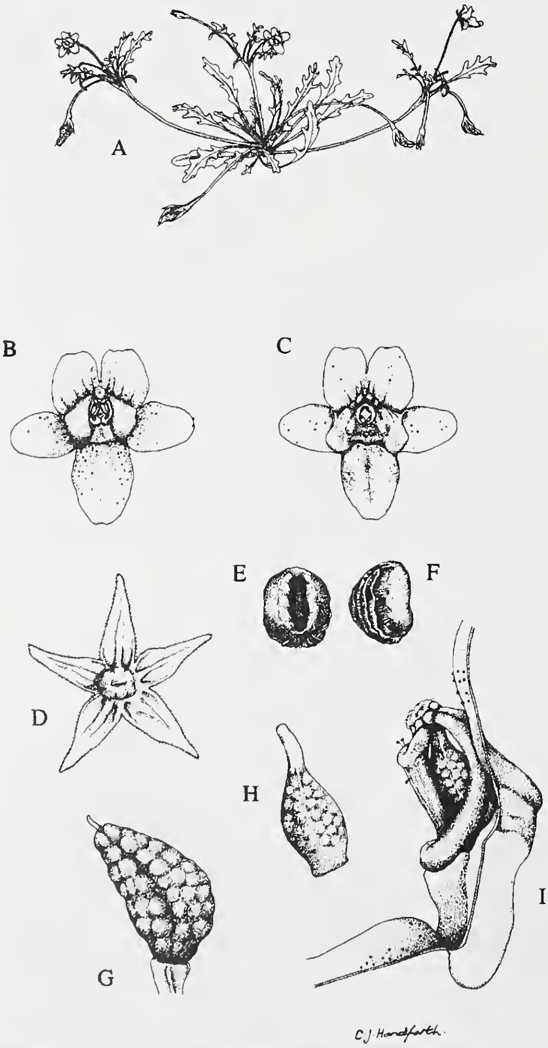

FIGURE 3.—*Diascia humilis, Steiner 2119.4*: A, habit, × 0.7; B, flower, front view, × 3.5; C, flower, rear view × 3.5; D, calyx × 5.5; E, seed, ventral view, × 17.5; F, seed, side view, × 17.5; G, capsule, × 4.2; H, gynoecium, × 11.4; I, androecium, × 11.4.

found on burned sites. It can be distinguished from that species most easily by the configuration of its stamens. In *D. maculata* the stamens project forward away from the upper corolla lip, whereas in *D. humilis*, they are erect with the anthers in a position very close to the upper corolla lip. The yellow markings on the two species also differ. The sacs and sides of the boss in *D. humilis* are yellow, but there is no discrete spotting pattern as in *D. maculata*. In *D. maculata* there are one or several yellow spots at the base of each upper corolla lobe in addition to the yellow spot(s) at the base of the lateral lobes. Associated with the yellow spots at the base of each upper lobe in *D. maculata* is a patch of oil-secreting trichomes. *D. humilis* does not have such trichomes in this position. In *D. humilis* they are contained within each yellow sac.

Distribution and habitat: *D. humilis* ranges from the Kamiesberg south to Worcester and east through the Little Karoo to Uniondale (Figure 2). It ranges in elevation from 320 to ± 1 200 m and is most commonly found on first year renosterveld or fynbos burns, however it also occurs in short karroid shrublands.

Breeding system: *D. humilis* is autogamous; but like *D. maculata* it secretes floral oil and may therefore be visited and cross-pollinated, at least occasionally, by small, short-legged, oil-collecting *Rediviva* bees (cf. Steiner & Whitehead 1988, 1990, 1991; Whitehead & Steiner 1985).

CAPE.—3018 (Kamiesberg): Farm Welkom, 6.4 km south of junction with Garies–Platbakkies Road, (–AC), 1 130 m, 29-ix-1988, *Steiner 1837* (NBG). 3119 (Calvinia): Lokenburg, (–CA), 29-viii-1941, *Compton 11501* (NBG); Botterkloof Pass, (–CD), 16-viii-1983, *Batten 660* (E); Farm Koerdemoefontein, 5.9 km E of Oorlogskloof road on road to Clanwilliam (R364), (–CD), ± 720 m, 15-ix-1989, *Steiner 2005* (NBG). 3219 (Wuppertal): road to Wuppertal, 3.9 km south of turnoff to Doringrivier in Bidouw Valley, (–AA), 500 m, 29-viii-1990, *Steiner 2204* (NBG); pass into Bidouw Valley, 6.2 miles from turnoff from Clanwilliam–Calvinia road, (–AA), ± 470 m, 24-viii-1967, *Thompson 348* (STE); Krom River, S Cedarberg, (–CB), 2-x-1952, *Esterhuysen 20469* (BOL). 3220 (Sutherland): Farm Driefontein, 7.2 km east of turnoff to Ouberg Pass on road to Ladismith, (–CB), 850 m, 6-viii-1990, *Steiner 2119* (NBG); ± 15 m north of road 356, 86.7 km NE of road 355, Farm Thyskraal, (–CC), 840 m, 26-ix-1984, *Steiner 793* (NBG). 3319 (Worcester): Farm Matroosberg, Hex River Pass, ± 5 km east of turnoff to De Doorns on N1, (–BD), ± 710 m, 3-x-1989, *Steiner 2034* (NBG); ibid., 18-x-1989, *Steiner 2049* (NBG); Breede River flood plain behind shooting range on Worcester commonage, (–CA), 220 m, 9-ix-1985, *Steiner 1010* (NBG). 3320 (Montagu): Touwsrivier, on hill ± 2 km west of Tweedside railway station, (–AB), 1 200 m, 12-viii-1988, *Vlok 1990* (NBG); Farm Driefontein, 7.2 km east of turnoff to Montagu on Touwsrivier–Ladismith road, (–CB), 850 m, 6-viii-1990, *Steiner 2119* (NBG); Farm Rietvlei, Montagu–Barrydale Road (R62), ± 10.5 km SE of Montagu, (–CC), ± 370 m, 18-viii-1987, *Steiner 1501* (NBG); Kogmanskloof, 100 m north of tunnel on Ashton–Montagu road, (–CC), 180 m, 8-ix-1984, *Steiner 740* (pressed ex hort), 2-xi-1984 (NBG); Montagu–Barrydale road, (R62), 16.5 km west of turnoff to Tradouw's Pass in Barrydale, (–DC), ± 540 m, 18-viii-1987, *Steiner 1507* (NBG). 3322 (Oudtshoorn): Farm Swartberg, lower northern slopes of Swartberg Mts, (–AD), ± 1 030 m, 12-ix-1986, *Vlok 1605* (NBG). 3323 (Willowmore): Farm Misgund, at southern base of Antoniesberg, (–AD), ± 905 m, 24-viii-1990, *Vlok 2383* (NBG).

D. hexensis *K.E. Steiner*, sp. nov., *D. sacculatae* Benth. affinis , sed differt floribus maioribus, calcaribus corollae deorsum curvis (non sursum curvis) et longioribus (9.5–11.5 mm, non <4.0 mm).

TYPE.—Cape, 3319 (Worcester); near top of Hex River Pass, 17.3 km west of junction with road R46 to Ceres, (–BD), ± 780 m, 20-ix-1985, *Steiner 1042* (NBG, holo.; MO). Figure 4.

Annual herb, glabrous, simple or branching from the base. *Stems* up to 220 mm long, erect or decumbent, tetragonal in cross section, up to 1.5 mm on a side. *Basal leaves* few to many, rosulate or crowded, simple, petiolate; lamina 8–34 mm long, ovate or obovate to elliptic, apex rounded to acute or apiculate, base attenuate, margins irregularly toothed or occasionally lobed or cleft, lobes or teeth narrowly to broadly triangular, acute to apiculate; petioles up to ± 20 mm long; stem leaves opposite, alternate or verticillate, becoming reduced upwards. *Flowers* axillary, one flower open per stem, unscented, nodding in bud, pedicels 25–80 mm long, ascending, broadened and dorsiventrally flattened especially where attached to the flower, elongating and ascending or recurved with only the apical portion ascending in fruit. *Calyx* lobes five, upper three ± equal, ± 3.1–4.0 × 0.8–1.2 mm, reflexed, lower two somewhat broader ± 3.1–4.1 × 1.2–1.4 mm, spreading, all lobes lanceolate, attenuate with white ciliate margins. *Corolla* bilabiate, limb ± 11.0–15.3 × 12.9–17.0 mm; upper lobes ± 3.6–4.7 × 4.2–5.0 mm, widely ovate to oblong-ovate, rounded to emarginate, bases oblique, lateral lobes ± 4.9–5.1 × 3.8–4.8 mm, oblong-ovate, rounded to emarginate, lower lobe ± 4.8–6.4 × 5.8–8.3 mm, obcordate, all lobes purple to reddish purple on front and pale purple on back, upper lobes with several darker reddish purple lines at the base, glandular pubescent especially on inside surface; tube, ± 1.0 mm deep, purple to reddish purple inside with 2 or 3 small fusiform to elliptic yellow spots at the base of each upper corolla lobe, spots on outside larger, one or two small ones and one large one or sometimes all confluent and forming a single large

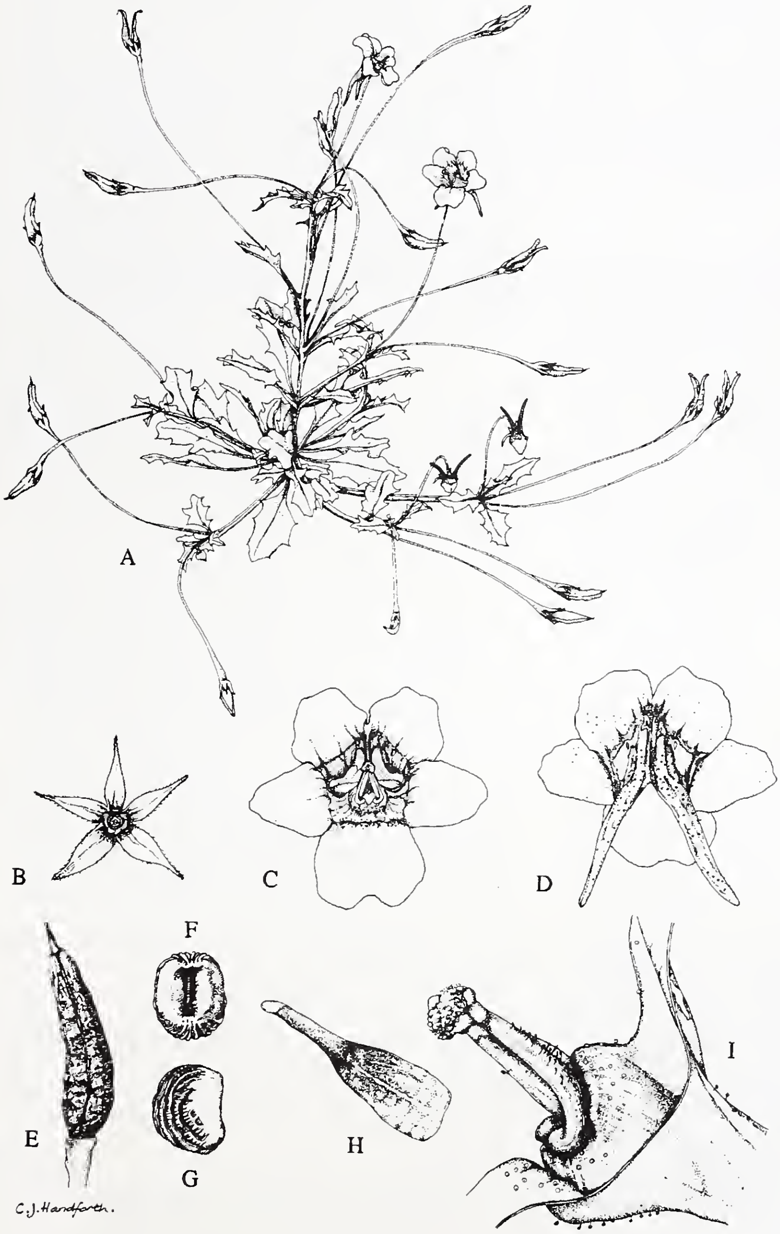

FIGURE 4.—*Diascia hexensis*, *Steiner 2117.2*: A, habit × 0.7; B, calyx, × 2.9; C, flower, front view, × 2.6; D, flower, rear view, × 2.6; E, capsule, × 2.9; F, seed, ventral view, × 18.4; G, seed, side view, × 18.4; H, gynoecium, × 8.8; I, androecium, × 8.8.

spot, tube drawn out below upper lip into 2 spurs ± 9.5–11.5 mm long (measured along the inseam), diverging, projecting backwards and downwards, attenuate, purple to reddish purple, containing clear to light purple, spherical, multicellular, oil-secreting trichomes in the distal half, sparsely glandular pubescent outside, tube at base of lower lip turned out to form a boss bearing the stamens, boss ± 1.0–1.3 mm high on the anticous side and 1.3–1.6 mm high posticous to the stamens, with scattered glandular hairs, connected on the posticous side to the upper lip by a septum. *Stamens* four, projecting forwards, filaments light purple, anticous filaments (appearing posticous due to twisting of the bases) ± 3.0–3.5 mm long, curved at the base, with scattered purple clavate trichomes on the upper portion, posticous filaments (appearing anticous) ± 2.5–2.9 mm long, ± straight, glabrous or with a few purple clavate trichomes; anthers ± 0.3–0.5 mm long, strongly cohering, yellow. *Ovary* ± 1.75–2.1 × 1.0–1.1 mm, oblong-ovate in outline, style ± 1.5–1.8 mm long, ± straight, stigma subcapitate, surrounded by anthers, ovules ± 90–100. *Capsule* ± 8.7–10.5 × 2.2–2.6 mm, narrowly falcate, ± twice as long as the calyx at maturity, seeds ± 0.7–0.8 mm long, falciform in outline, dorsal surfaced ridged, ventral surface with seed coat extended to form a cupule with an oblong opening.

Flowering time: August–October.

Diagnostic features: *D. hexensis* is most easily recognized by its moderately long attenuate corolla spurs, its long narrowly falcate capsule (± 3.5 to 4.5 times as long as wide) and its ovate broadly toothed leaves. Although capsule and leaf shape are similar in *D. sacculata*, the much longer spurs of *D. hexensis* clearly distinguish it from that species.

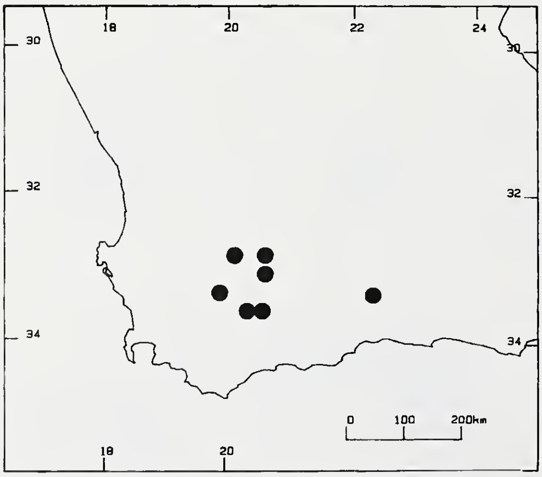

FIGURE 5.— Known distribution of *Diascia hexensis* in South Africa.

Distribution and habitat: *D. hexensis* is known only from the southern part of the Roggeveld Mountains west of Sutherland, south to the northern slopes of the Langeberg (Figure 5). It ranges in elevation from 510 m to 1 300 m and occurs in karoo shrublands on relatively moist south-facing slopes. The specific epithet refers to its occurrence next to the Hex River Pass.

Breeding system: *D. hexensis* is autogamous; but because of its long spurs containing floral oil, it is probably visited and cross-pollinated, at least occasionally, by medium-sized oil-collecting *Rediviva* bees with long forelegs.

CAPE.—3220 (Sutherland): Ouberg Pass road, 0.7 km west of Vis River rd, 1 300 m, (–AD), 1-x-1986, *Steiner 1409* (NBG); ± 15 m north of road 356, 86.7 km NE of R355, Farm Thyskraal, (–CC), 840 m, 26-ix-1984, *Steiner 790* (NBG); below road to Sutherland (R354), 45.1 km north of junction with National Road (N1) at Matjiesfontein, (–DC), ± 900 m, 20-ix-1985, *Steiner 1053* (NBG). 3319 (Worcester): Farm Matroosberg, Hex River Pass, ± 5 km east of turnoff to De Doorns on N1, (–BD), ± 710 m, 3-x-1989, *Steiner 2032* (NBG). 3320 (Montagu): Whitehill, (–BA), 18-viii-1941, *Compton 11249* (NBG); Farm Driefontein, 7.2 km east of turnoff to Ouberg Pass on road to Ladismith, (–CB), 6-viii-1990, *Steiner 2117* (NBG); Farm Sewefontein, 32 km west of Ladismith–Laingsburg road, (–DA), 510 m, 6-viii-1990, *Steiner 2125* (NBG). 3322 (Oudtshoorn): Farm Frisgewaagd, northern slopes of the Swartberg (–AD), ± 1 000 m, 12-ix-1986, *Vlok 1604B* (NBG).

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Studies in the genus *Riccia* (Marchantiales) from southern Africa. 24. *R. moenkemeyeri*, subgenus *Ricciella*: new records

S.M. PEROLD*

Keywords: Marchantiales, *Riccia moenkemeyeri*, southern Africa, subgenus *Ricciella*

ABSTRACT

Riccia moenkemeyeri was twice described by Stephani (1887, 1891), the second time as *R. abnormis*. Arnell (1952) described it as *R. undulata*. It is clearly a plastic species (Jones 1957) and is widely distributed in tropical Africa, from Sierra Leone (as *R. undulata*), Nigeria, Cameroon and into the Congo Basin. Until recently, Sim's specimens from the Matopos in Zimbabwe, were the most southerly records known, but the species has now also been collected in southern Africa, just east of Pretoria and at Kransberg, in the western Transvaal.

UITTREKSEL

Riccia moenkemeyeri is twee keer deur Stephani (1887, 1891) beskryf, die tweede keer as *R. abnormis*. Arnell (1952) het dit as *R. undulata* beskryf. Dit is duidelik dat dit 'n variërende spesie is (Jones 1957), wydverspreid in tropiese Afrika, vanaf Sierra Leone (as *R. undulata*), Nigerië, Kameroen en tot in die Kongo-bekken. Tot onlangs, was Sim se eksemplare afkomstig van die Matopo-heuwels in Zimbabwe, die mees suidelike rekords bekend, maar die spesie is nou ook in Suider-Afrika net oos van Pretoria en by Kransberg, in Wes-Transvaal, versamel.

Riccia moenkemeyeri *Steph.* in Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie 8: 95 (1886 '1887'); Steph.: 372 (1898); Jones: 211 (1957); Vanden Berghen: 189 (1972). Type: Niger Gebiet, Alt Calabar in terra, leg. *Moenkemeyer N3*, 11-10-1884 (G024384, holo.!; S, iso.)

R. abnormis Steph.: 213 (1891); ibid.: 364 (1898). Type: Kamerun, Bateki, leg. *P. Dusén 125*, 17 Oct. 1890 (G).

?*R. chevalieri* Steph.: 116 (1912); ibid.: 1 (1917). Type: Central African Republic, Haut-Oubangui, Plateau des Ungourras, 650 m, Nov. 1902, leg. *Chevalier*, ex Herb. Corbiére.

Ricciella undulata S. Arnell: 105 (1952). Type: Africa occidentalis, Sierra Leone, Freetown, stream-side above Calabar Point, *S. Arnell 2252* (S).

Thallus monoicous, annual, in crowded and often overlapping, gregarious patches; glaucous green, turning white over older parts and along undulating margins, sometimes with purple-red band on inner side; medium-sized to fairly large; branches once to several times furcate, closely to moderately divergent (Figures 1A; 2A), up to 9–10(–12) mm long, segments 2.0–5.0 × 1.6–2.5 mm, 0.8 mm thick medianly but thinner toward margins, ± 2–3 times wider than thick in section (Figure 1E), oblong to ovate, apex rounded to subacute, emarginate, dorsally deeply grooved distally (Figure 2B), becoming shallowly grooved to flat or concave proximally; thallus margins rapidly thinning, acute, winged and attenuate, ultimately consisting of a single row of echlorophyllose cells; flanks green to purple-red below, and rather steep, then abruptly sloping obliquely upward and outward (Figure 1E), becoming white toward margin; ventrally rounded, green, sometimes apically with 1 or 2 rows of vestigial red scales (Figure 1B); when dry (Figure 1C) concave dorsally, margins apically incurved to inflexed or somewhat recurved.

Anatomy: dorsal epidermis chlorophyllose, forming numerous small, slightly domed to flat areas, generally enlarging toward margins and proximally, sometimes rupturing and partly exposing the air chambers below, cells polygonal, 42–55 × 20–37 μm, surrounding a central, 4- or 5-sided air pore (Figure 1D; 2D), mostly only ± 12.5 μm wide toward apex, pores enclosed by smaller companion cells, ± 15 × 10 μm; assimilation tissue 350–400 μm thick, nearly ½ the thickness of thallus, air chambers about 24 across width of thallus, centrally narrow and vertical, 50–60 μm wide, somewhat wider laterally and sloping obliquely, uniseriate, but in transverse section (Figure 1E) often appearing to be secondarily partitioned due to forward or lateral inclination, enclosing cellular unistratose plates, cells irregular in shape and size, 32–87 × 25–37 μm (Figure 1F); storage tissue 400–450 μm thick, slightly more than ½ the thickness of thallus, cells averaging 50 μm in width, containing angular, closely packed starch granules, but with small spaces wedged in between; rhizoids smooth or tuberculate, ± 15 μm wide. *Scales* mostly quite firmly attached to flanks and difficult to detach, dark wine-red and shiny or hyaline, not extending to thallus margins (Figure 2C), spaced, cells polygonal, 50–75 × 30–45 μm.

Antheridia in a row along groove (Figure 1A), hyaline necks emerging from small depressions, 200–295(–375) μm long. *Archegonia* median, deeply imbedded, obliquely orientated, necks sloping toward the apex of the thallus, up to ± 300 μm long, upper part hyaline and basally purple, difficult to detect from above. *Sporangia* oblique and protruding ventrally (Figure 1G), single or 2 adjacent or serially arranged, subspherical, ± 500 μm wide, containing 145–190 spores each. *Spores* (65–)68–75(–85) μm in diameter, triangular-globular; polar, light tan to yellowish brown, semitransparent; wing ± 5 μm wide, slightly wider at generally perforated marginal angles, margin finely crenulate; ornamentation reticulate, but completely dissimilar on 2 spore faces: distal face (Figure 2E)

* National Botanical Institute, Private Bag X101, Pretoria 0001.
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with (8)9 or 10 areolae across diameter, 8–10(–12) μm wide, occasionally incompletely separated, walls low, covered with fine granules and slightly raised into papillae at nodes; proximal face lacking a triradiate mark, but each of 3 facets with up to ± 100 tiny, mostly less than 2.5 μm wide, shallow, but clearly defined areolae, the walls forming a fine network (Figure 2F). *Chromosome number*: n = 9 (Figure 1H) (Bornefeld on *S.M. Perold 2603* pers. comm.); n = 8 (Jovet-Ast 1969).

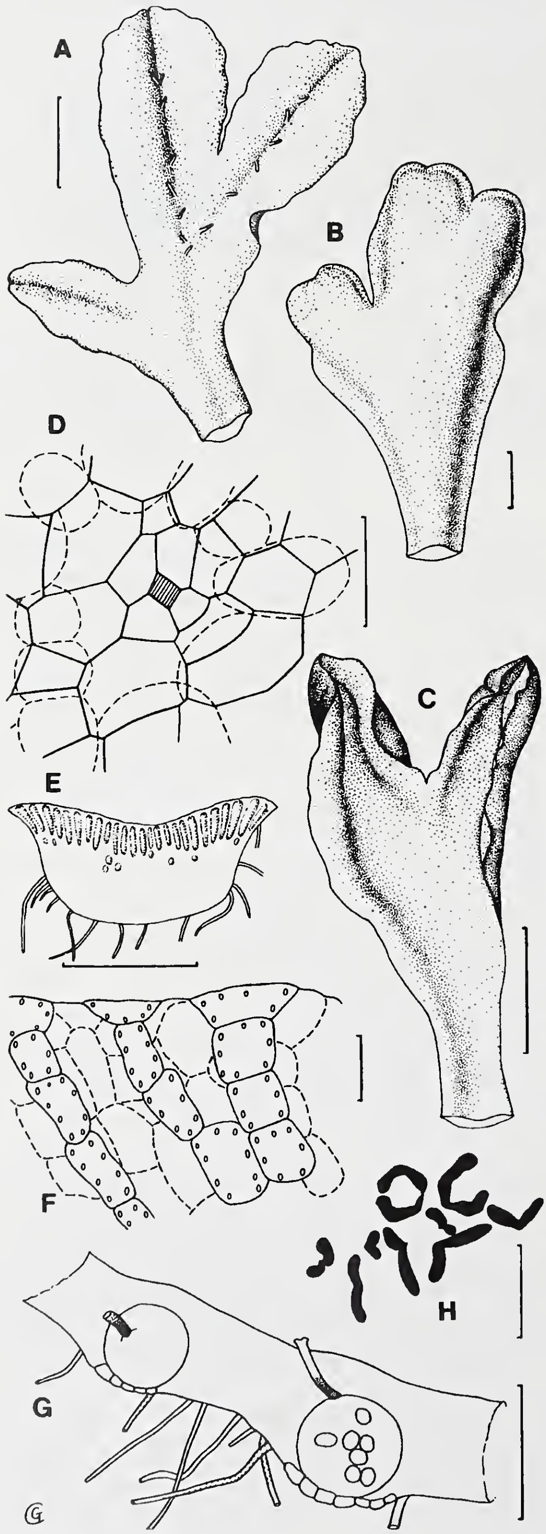

FIGURE 1.—*Riccia moenkemeyeri*. Morphology and anatomy. A–C, thallus: A, dorsal face, turgid, with rows of antheridial necks; B, ventral face; C, dry. D, air pore (crosshatched) dorsal, subdorsal cells (stippled lines) enclosing air chamber. E, t.s. of branch; F, t.s. of part of thallus showing air chambers; G, l.s. of sporangium with forward sloping neck; H, chromosomes. A–H, *S.M. Perold 2603*. Drawings by G. Condy; karyotype by T. Bornefeld. Scale bars on A–C, F, G = 1 mm; D, F = 50 μm; H = 1 μm.

Riccia moenkemeyeri is a tropical African species, known from Sierra Leone (as *R. undulata*), Ghana, Nigeria, Cameroon, the Congo Basin, (Région du Lac Moero (Vanden Berghen 1972)), Angola, Zimbabwe, Malawi, and now also with outliers into the Transvaal, southern Africa (Figure 3). Its presence on Fernando Po, as reported by Stephani (1887) for the type specimen, *Moenkemeyer 3*, must have been a mistake, as the locality on the label states that it is from Calabar, Niger, and in *Species hepaticarum* (Stephani 1898) it also does so.

The species grows in damp places, on rich loamy soil, mostly near streams and in association with other *Riccia* species (in southern Africa) such as *R. stricta* (Lindenb.) Perold, *R. atropurpurea* Sim and with *Exormotheca pustulosa* Mitt.

Riccia moenkemeyeri is characterized by a more or less persistent dorsal epidermis which is marked out into small areolae, each with a small central air pore; by numerous, narrow air chambers, appearing to be in more than one layer; by undulating thallus margins which terminate in a single row of hyaline cells and by a highly distinctive spore ornamentation with 8–10 large areolae on the distal face and numerous tiny areolae on the proximal face which lacks a triradiate mark.

According to the classification used in previous papers in this series, *R. moenkemeyeri* is placed in subgenus *Ricciella*, section *Spongodes*, on account of the presence of air chambers in the assimilation tissue. Although not truly growing in rosettes, it would be more properly placed in the informal group ‘Crystallina’, together with *R. crystallina* L. emend. Raddi, *R. cavernosa* Hoffm. emend. Raddi and *R. cupulifera* A.V. Duthie, than in group ‘Vesiculosa’ with *R. bullosa* Link ex Lindenb., *R. garsidei* Sim, *R. volkii* S. Arnell and *R. rubricollis* Garside & Duthie ex Perold, which mostly have rather ‘swollen’ thalli with large, inflated air chambers. The oblique orientation of the ventrally protruding sporangia is a character which it apparently shares only with *R. stricta* (Lindenb.) Perold, but the latter species has long, narrow, ribbon-like branches and is placed in subgenus *Ricciella*, section *Ricciella*.

The specimen, *S.M. Perold 2603*, collected in March 1990, appeared to consist of male plants only, but on serial and longitudinal sections of several branches, it was found to also have young, deeply imbedded archegonia with long necks that are, however, not visible from above. Mature antheridia have necks up to 375 μm long, but in young antheridia they are considerably shorter. Dr E.W. Jones

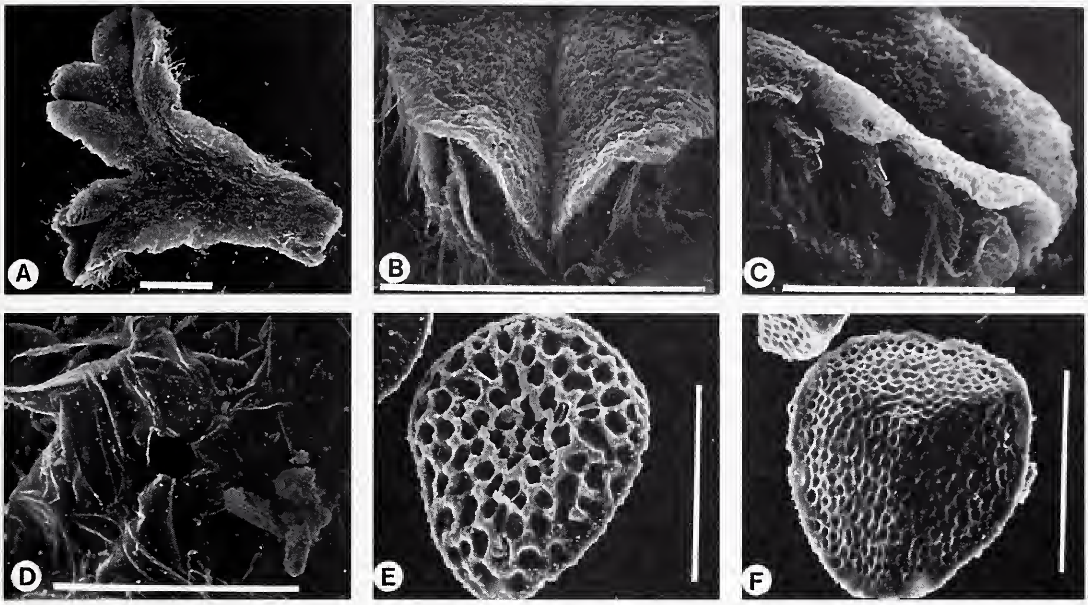

FIGURE 2.—*Riccia moenkemeyeri*. Morphology and spores. A, thallus; B, apex with groove and scales; C, apical scales seen from the side; D, air pore; E, distal face of spore; F, proximal face of spore. A–D, *S.M. Perold 2603*; E, F, *T.R. Sim 9072*. Scale bars on A–C = 1 mm; D–F = 50 μm. SEM micrographs by S.M. Perold.

kindly examined part of my collection and commented on the antheridial necks being shorter than 100 μm. He also found (pers. comm.) that West African specimens of *R. moenkemeyeri* are only exceptionally without spores, the branches are longer and less divaricate and the epidermis is more persistent. The *Condy 22* and *23* collections were gathered in April 1991, (slightly later in the following season than my specimen) and both had sporangia with mature spores. Seventeen months after collection, a sample of *S.M. Perold 2603* was kept damp for a few days in a Tupperware dish and it soon resumed growth.

Jones (1957) reported *R. moenkemeyeri* to be a very plastic species, a wide range of forms occurring in a single site. He regarded *R. chevalieri* Steph. as closely resembling *R. moenkemeyeri* in vegetative features; the type specimen, *Chevalier 88*, however, only had 'a few male inflorescences but no female', and its identification could thus not be confirmed by spore ornamentation.

Riccia undulata S. Arnell was placed in synonymy under *R. moenkemeyeri* by Jones (Jones & Harrington 1983), although Arnell (1952) reported the fronds to be up to 7 mm wide, which is much wider than the measurements (2.0–2.5 mm) given by Jones (Jones & Harrington 1983) for the type specimen. The spores of the two species are identical, however.

Jovet-Ast (1975) reported on spore germination and development of the protonema in *R. moenkemeyeri*, concluding that the various stages (quadrant, plate and column formation) were similar to those in *R. cavernosa*.

The reason for the discrepancy in the chromosome counts of *R. moenkemeyeri* as reported by Bornefeld (pers. comm.) and Jovet-Ast (1969), has not been ascertained. Jovet-Ast maintains that in *Riccia, n* always equals 8 or multiples of 8. Jovet-Ast (pers. comm.) expressed surprise that Bornefeld's (1989) counts do not agree with hers and suggests that Bornefeld's counts be verified. Bornefeld (1984) postulates that the different chromosomes of the basic set in *Riccia*, which he identifies as A, BB, CC, DD and E, can multiply heterogeneously (for which he has coined the term 'nothopolyploidy'); this would explain how aberrant numbers could arise.

SPECIMENS EXAMINED

TRANSVAAL.—2528 (Pretoria): 18 km NE of Cullinan, north of Little Eden Resort, nr 'Die Grotte', Malanspruit, next to river path, on soil below overhanging rock, (–DA), *S.M. Perold 2603* (PRE). 2427 (Thabazimbi): Kransberg, at seasonally flowing stream, south-facing bank under rock, (–BC), *Condy 22* (PRE); Kransberg, near rondavel, below stream crossing, at water's edge among ferns, (–BC), *Condy 23* (PRE).

ZIMBABWE.—[previously misidentified and reported as *R. albomarginata* (Best 1990)] 2028 (Bulawayo): stream at Bulawayo, (–?AA), *T.R. Sim 9069 (PRE-CHI015)* (PRE); Matopos, (–CA), *T.R. Sim 9068*

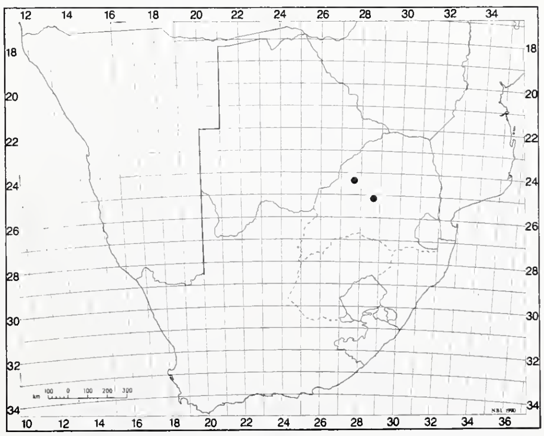

FIGURE 3.—Map showing distribution of *R. moenkemeyeri* in southern Africa.

(CH 1014) (BOL, PRE). 2030 (Masvingo): (—BB), *T.R. Sim 9070 (PRE-CH1012), 9072 (PRE-CH1013)* (PRE).

MALAWI.—1434: 31 km E of Lilongwe, on road to Zomba, on left side of road, beyond legume patch, on damp soil of footpath leading to flat rocks, (—AA), *S.M. Perold 2690* (PRE). 1535: at roadside in Zomba, damp earth wall nr river, (—AD), *S.M. Perold 2655* (PRE).

ANGOLA.—Dist. Pungo Andongo, hab. gregaria ad cavernas rup. editiorum in Pedra de Cazella ipsius Praesidii, *Welwitsch 229* (as *R. abnormis*) (BM); Dist. Golungo Alto, habit ad rupes limosas rivuli, Carenghe in Alto Queta, *Welwitsch 309a* (BM); Dist. Golungo Alto, ad terram humidam juxta Rivuli de Quarengue in Queta, *Welwitsch 309b* (BM).

BELGIAN CONGO.—*Léonard 11894, 11895* (BR).

CAMEROON.—Cap Debunsch, *J.S. Jungner 1891* (NY); Bipinde, Urwaldgebiet, *G. Zenker 2431h* (as *R. abnormis*) (BM, E); *P. Dusén s.n.* (as *R. abnormis*) (BM).

NIGERIA.—Ibadan University Bot. Garden, on moist sand under large trees near the river, *E.W. Jones 1187*; Calabar, sandy roadside ditch near the harbour, *E.W. Jones 209*; Sanga River Forest Res., Kurmi Kadar, on very wet heavy red loam on bank of small stream, still flowing at end of dry season, *E.W. Jones 927*; Abuja, on earth of rocky bank in shade of trees by the Rest House, *E.W. Jones 893* (all at Herb. Jones).

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Aspidonepsis (Asclepiadaceae), a new southern African genus

A. NICHOLAS* and D.J. GOYDER**

Keywords: *Asclepias*, Asclepiadaceae, *Aspidonepsis*, new genus, new species, southern Africa, taxonomy, *Unguilobium*

ABSTRACT

Aspidonepsis, an endemic southern African genus, is described and compared to the closely allied genus *Aspidoglossum*. This newly described genus is composed of two subgenera, **Aspidonepsis** and **Unguilobium**, consisting of three and two species respectively. *Asclepias diploglossa, A. flava, A. cognata* and *A. reneensis* are transferred to **Aspidonepsis**, and **A. shebae** is newly described. All species are discussed, illustrated and a key is given to aid in their identification.

UITTREKSEL

Aspidonepsis, 'n genus endemies in suidelike Afrika, word beskryf en met die naverwante genus *Aspidoglossum* vergelyk. Die nuut beskrewe genus bestaan uit twee subgenusse **Aspidonepsis** en **Unguilobium**, met drie en twee spesies onderskeidelik. *Asclepias diploglossa, A. flava, A. cognata* en *A. reneensis* word na **Aspidonepsis** oorgeplaas, terwyl **A. shebae** nuut beskryf word. Al die spesies word bespreek, geïllustreer en 'n sleutel om te help met hul identifikasie, word gegee.

INTRODUCTION

A.A. Bullock's work on the family Asclepiadaceae (1952 to 1967) has received wide acceptance in Africa north of the Limpopo River. In southern Africa, however, his generic concepts and names have seldom been applied. This is explained partly by the fact that his research seldom included southern African plants and partly by the rejection of his work by Dyer (1975).

Unfortunately, three elements detract from Bullock's work: 1, he admitted that his delimitation of genera was only tentative (1952); 2, when resurrecting or expanding existing genera he seldom gave new descriptions for these taxa. As a result, the generic circumscriptions and exact application of some of these names is still unclear; 3, his species concepts were often very broad and there is now growing consensus that some species will need to be re-split.

Most southern African herbaria therefore still follow N.E. Brown's treatment of the Asclepiadaceae as outlined in the *Flora capensis* (1907–1909). However, workers like N.E. Brown had followed the tradition of their time and separated genera using floral differences only. They even separated some genera on the basis of a single character. Phenomena like convergent evolution were seldom taken into account, and workers were unaware that the evolution of analogous floral morphologies had taken place within the family. Bullock (1952) was the first to realize that such convergent evolution had taken place and that many genera in the family not only contained a number of unrelated entities, but that these entities could only be identified in terms of consistently produced correlated character combinations. He was the first taxonomist to attempt a phylogenetically based classification for the African members of the tribe Asclepiadeae.

What Bullock has done at the generic level, N.E. Brown has accomplished at the specific level. Consequently the work of N.E. Brown (species delimitation) and Bullock (generic delimitation) should be seen as complimentary rather than antagonistic.

Recent investigations concerning the southern African members of the genus *Asclepias sensu* N.E. Brown have shown that Bullock's generic concepts should be redefined and extended to embrace the taxa of this subcontinent (Nicholas 1981). Bearing in mind that the type species of the genus *Asclepias* L. is *A. syriaca* L., the authors agree with Bullock in the exclusion of *Asclepias* from Africa except as an adventive. The process of moving the southern African taxa of *Asclepias sensu* N.E. Brown to their correct generic position has already begun (Nicholas & Goyder 1990). The authors understand the desirability of giving a brief generic synopsis of the subtribe Asclepiadineae in Africa at this early stage of their work. However, as a number of genera still need to be: 1, resurrected from synonomy; 2, newly described; 3, extensively redefined; they feel that it is at present unwise to publish information that may change as their research progresses.

Aspidonepsis diploglossa (Turcz.) A. Nicholas & D.J. Goyder, *A. flava* (N.E. Br.) A. Nicholas & D.J. Goyder, *A. cognata* (N.E. Br.) A. Nicholas & D.J. Goyder, *A. reenensis* (N.E. Br.) A. Nicholas & D.J. Goyder and *A. shebae* A. Nicholas & D.J. Goyder form a phylogenetic unit quite distinct from the rest of *Asclepias sensu* N.E. Brown and can be distinguished from other genera in the tribe Asclepiadeae by the following set of consistently present correlated characteristics:

1, a globose, fusiform or napiform tuber just below the soil surface;
2, a single erect stem (rarely up to 3 in *A. flava*);
3, spreading to ascending linear to narrowly elliptic leaves which are ranked up the stem;
4, inflorescences gathered together at the top of the flowering stem, even if nodally produced;

* National Botanical Institute, Private Bag X101, Pretoria 0001. Formerly: South African Liaison Botanist, Royal Botanic Gardens, Kew, Richmond, Surrey TW9 3AE, England, UK.
** The Herbarium, Royal Botanic Gardens, Kew, Richmond, Surrey TW9 3AE, England, UK.
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5, persistent inflorescence bracts, often grading with the leaf system;
6, cucullate corona lobes which are produced 0.5 to 1.8 mm above the insertion of the corolla;
7, a saccate corona lobe cavity;
8, wishbone-shaped pollinaria, with semicircular to hemi-ovoid pollinia.

Aspidonepsis is confined to high altitude grasslands of the Drakensberg and its foothills, although outlying populations of some species may be found in mountainous situations as far south as Grahamstown and on montane 'islands' nearer the Transkei-Natal coast. The northern limit of distribution of this endemic southern African genus is the eastern Transvaal. Species are usually, but not always, found in situations subject to annual burning. Populations are intermittent in the wild and usually consist of few widely dispersed individuals. Occasionally up to three tubers are produced in a connected series, possibly representing subsequent year's growths.

Aspidonepsis bears a number of similarities to the genus *Aspidoglossum* (Table 1), and it is the authors' opinion that the two genera may have originated from the same distant, ancestral stock. However, if this is the case, then the two taxa have since evolved along very different lines, for a number of major disjunctions in morphology now exist, such as the aggregation of inflorescences near the stem apex and the central cavities in the corona lobes of *Aspidonepsis*. In contrast *Aspidoglossum* bears inflorescences that are produced along the length of the stem and there is no corona lobe cavity.

The affinity of these two genera can be clearly seen in the corona lobe and pollinarium morphology of *Aspidoglossum delagoense* (Schltr.) Kupicha, which is very similar to *Aspidonepsis* (Figure 1). However, all other features of this species place it clearly within *Aspidoglossum*, of which *A. biflorum* E. Mey. is not only the type species but also typical of the genus as a whole (Kupicha 1984). *Aspidoglossum* has more species and is morphologically more diverse than *Aspidonepsis*.

The five species recognized in *Aspidonepsis* fall into two well-defined groups that require recognition at subgeneric level. The first group is characterised by spreading or ascending corolla lobes and cup- or dish-shaped corona lobes with a tooth-like appendage projecting from the floor of the corona lobe cavity. The second group has reflexed corolla lobes and corona lobes with a more angled outer margin and no tooth-like structure projecting from the floor of the corona lobe cavity.

A total of 187 pressed specimens were examined during the course of this study from the following herbaria: BOL, CPF, GRA, J, K, NBG, NH, NU, PRE, SAM and TCD*. Additional data were obtained from spirit collections and supplemented by observations in the field.

* Herbarium abbreviations are taken from Holmgren *et al.* (1990).

TAXONOMY

Aspidonepsis *A. Nicholas & D.J. Goyder*, gen. nov., *Aspidoglosso* affinis sed sinu coronae lobis prominenti et appendice distali coronae lobis non filiformi nec ornata differt.

Herba perennis. *Caudex*: tuber globosum, fusiforme vel napiforme. *Caulis* unicus (raro duo vel tres), erectus, gracilis, usque 625 mm tantum longus. *Folia* expansa, anguste elliptica vel linearia in subgenere *Aspidonepse*, sed ascendentia, linearia vel nonnunquam lanceolata, margine manifeste revoluta in subgenere *Unguilobio*. *Inflorescentia* umbellata, terminalis subterminalisve vel ad nodos disposita, 2–17-flora (in subgenere *Aspidonepse*), 4–11-flora (in subgenere *Unguilobio*); bracteae ad anthesin persistentes. *Coronae lobi* partibus inferioribus ad columnam staminalem connatis; 0.5–1.8 mm supra corollam producti, cucullati; sinus profundus appendice linguiformi centrali ornatus in subgenere *Aspidonepse*. Appendix proximalis ad apicem deltato-falcata et apicem stylii aequans vel superans impendensque; extremum distale coronae appendice parva ornatum vel appendice carente; sinus profundus rimiformis in subgenere *Unguilobio*. *Appendix antherae* reniformis vel pescapriformis profunde apicaliter fissa.

TYPUS.—*Aspidonepsis diploglossa* (Turcz.) A. Nicholas & D.J. Goyder, *vide infra*.

Perennial geophytic herb. *Rootstock* a globose, fusiform or napiform tuber. *Stems* 1 (rarely as many as three in *A. flava* only), erect, never more than 650 mm tall. *Leaves* spreading to ascending, linear, lanceolate to narrowly elliptic, older leaves shorter and broader; petiole

TABLE 1.—A comparison of *Aspidonepsis* and *Aspidoglossum*.

Character	*Aspidonepsis*	*Aspidoglossum*
Habitat	Montane only	Widespread
* Habit in the field	Erect	Erect but usually pendulous apically
Stem number	1, up to 3 in *A. flava*	Usually 1 to a few, occasionally many
Leaf insertion	Opposite	Opposite, or occasionally verticillate or irregular
Leaf shape	Usually linear, rarely lanceolate	Usually linear, rarely suborbicular, elliptic or obovate
* Inflorescence production	Near the stem apex only	Along the length of the stem, but also gathered apically
Inflorescence insertion	Not fascicled, rarely sessile	Fascicled, almost sessile near stem apex
* Flower colour	Yellow, purple, and brown	Purple and green, never yellow
* Corona lobe ornamentation	Appendages never complicate or filiform	Appendages either complicate & filiform or not ornamented
* Corona lobe cavity	Present	Not present, or rarely rudimentary
* Central corona lobe appendage	Within the corona lobe cavity	Present but not in the corona lobe cavity
Pollinaria shape	Wishbone-shaped	Wishbone-shaped or pachyform
Pollinia shape	Sausage-shaped	Sausage-shaped to pyriform

* important differences between the two taxa.

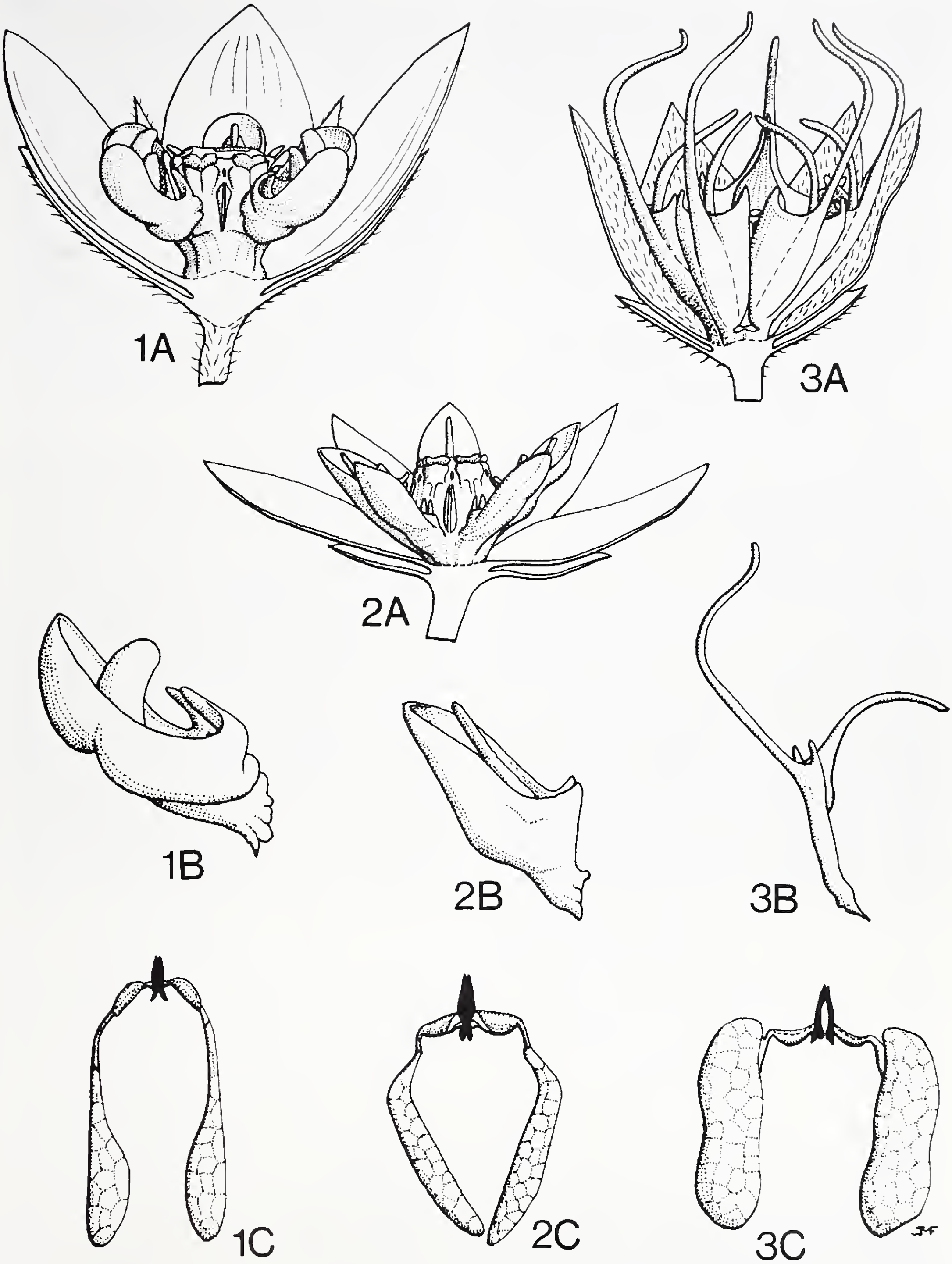

FIGURE 1.—Comparison of 1, *Aspidonepsis flava, Coleman 813*, (PRE); 2, *Aspidoglossum delagoense, Barbosa & De Lemos 7958*, (K); 3, *Aspidoglossum biflorum, Bolus 238*, (K). A, flower with part of corolla removed: 1A, × 11; 2A, × 9.5; 3A, × 7. B, corona lobe, side view: 1B, × 28; 2B, × 15; 3B, × 11. C, pollinarium: 1C, × 48; 2C, × 22; 3C, × 55.

0–5 mm long. *Inflorescences* umbelliform; terminal, subterminal and nodal; bracts present at anthesis. *Corolla* catilliform or reflexed with lobe apices ascending. *Corona* with lower parts fused to the staminal column; lobes produced 0.5–1.8 mm above the corolla, cucullate; cavity saccate with appendage (subgenus *Aspidonepsis*) or without appendage (subgenus *Unguilobium*). *Anther appendages* reniform to pescapriform, with a deep apical cleft, or rectangular. *Style*: head swollen; apex truncated. *Pollinaria* wishbone-shaped; corpusculum fusiform;

translator apparatus articulated and winged; pollinia semicircular to hemiovoid or clavate. *Habitat*: high altitude mountain grasslands. *Distribution*: southern African Drakensberg. *Etymology*: *Aspidonepsis = Aspidoglossum's* cousin. *Aspid(os)*, (Greek for shield) but used here to indicate the genus *Aspidoglossum*, and *anepsia* (Greek for cousin).

Key to subgenera and species

1a Corolla not fully reflexed when mature. Corona lobe cavity with a tongue-like appendage (Subgenus *Aspidonepsis*:
2a Proximal corona lobe appendages projecting over the style apex .... *A. cognata*
2b Proximal corona lobe appendages not projecting over the style apex:
3a Corona lobes with arm-like proximal appendages that cross over each other and reflex back into the coronal cavity. These appendages are below the style apex and level with the anther wings .... *A. flava*
3b Corona lobes without true proximal appendages, instead, the proximal ends are produced into dentate or obtuse (but not protruding) shoulders that are level with the style apex .... *A. diploglossa*
1b Corolla reflexed when mature. Corona lobe cavity without an appendage (Subgenus *Unguilobium*):
4a Distal corona lobe appendage present (if somewhat short). Transkei, Natal and southern Transvaal bordering Natal .... *A. reenensis*
4b Distal corona lobe appendage absent. Eastern Transvaal only .... *A. shebae*

ENUMERATION OF THE SUBGENERA AND SPECIES

A. Subgenus **Aspidonepsis**

Inflorescences 2–17-flowered. *Flowers* yellow, green, brown and purple or these in combination. *Corolla* catilliform with lobe apices curving upwards or spreading, lobes with abaxial surface glabrous. *Corona lobes*: upper proximal margin various, distal margin obtusely rounded or truncate and raised above the proximal appendages (except *A. diploglossa*); cavity saccate with a centrally produced laterally flattened tongue-shaped or botuliform appendage. *Anther appendages* reniform or pescapriform with a deep apical cleft. *Pollinia* narrowing proximally; translator arms in two distinct parts, winged (Table 2).

This subgenus is composed of three species: *Aspidonepsis diploglossa, A. flava* and *A. cognata*. For a number of years these three species were considered conspecific, and lumped together under the oldest name, viz. *A. diploglossa*. However, although all three species are vegetatively similar, close examination shows that they are distinct entities with very different floral morphologies (Nicholas 1987). They are usually found in annually burnt or grazed, high to medium altitude, montane grasslands. They are found along the Natal-Transkei Drakensberg, and on scattered island mountain ranges in the eastern Cape and Natal midlands. The flowers of this subgenus are predominantly yellow or yellow-green, although occasionally flowers with brown or purple markings can be found.

1. **Aspidonepsis diploglossa** *(Turcz.) A. Nicholas & D.J. Goyder*, comb. nov. Type: South Africa, Cape Province, peaks of the Winterberg, *Ecklon 23* (KW holo., photo!; PRE!, iso.).

Gomphocarpus diploglossus Turcz.: 258 (1848). *Asclepias diploglossa* (Turcz.) Druce: 605 (1917).

Asclepias schizoglossoides Schltr.: 32 (1894); Schltr.: 451 (1896); N.E. Br.: 688 (1908); Wood: 461 (1910); Phillips: 194 (1917). Type: South Africa, eastern Cape, *Mrs Barber s.n.* (K!, neo., here designated).

Rootstock 1 or several tubers connected in series, 9–35 × 6–12 mm. *Stems* 1, erect, 170–400(–500) mm tall, bifariously pubescent. *Leaves* ascending to spreading, narrowly lanceolate, occasionally falcate, rarely linear or narrowly elliptic, 5–84(–130) × (0.25–)0.5–7.0 mm; apex acuminate or occasionally acute; base petiolate to cuneate; apetiolate or petiole up to 4 mm long. *Inflorescences* 1–3 per plant, 4–16-flowered, bracts present at anthesis; peduncles up to 9.5 mm long or occasionally inflorescences apedunculate. *Flowers* 4–9 × 6–13 mm, yellow

TABLE 2.—A comparison of the two subgenera *Aspidonepsis* and *Unguilobium*. All measurements in mm

Character	*Aspidonepsis*	*Unguilobium*
Stem length	170–550	190–625
Leaf length	5–133	7–56
Peduncle length	0–175	5–90
Flower colour	Yellow, green, purple & brown	Yellow, purple & brown
* Corolla orientation	Spreading erect	Reflexed
Petal length	3.5–10.5	5.2–6.5
* Corona lobe shape	Cup-like (cucullate)	Claw-like (unguiform)
Proximal corona lobe appendage length	None–1.2	0.4–1.3
Distal corona lobe appendage length	None	None–0.5
* Corona lobe cavity appendage length	0.2–1.3	None
Alar fissure length	0.5–1.4	0.7–1.1
Anther appendage length	0.3–0.6	0.5–1.5
Style apex diameter	1.1–2.8	1.6–2.4
Translator arm length	0.18–0.56	0.28–0.64
Corpusculum length	0.16–0.32	0.2–0.4
Pollinium length	0.48–0.96	0.68–1.0

* characters forming discontinuities between the two taxa.

or yellow-brown; pedicel 6–16 mm long. *Calyx*: lobes lanceolate, occasionally triangular or narrowly ovate, 2.5–4.6 × 1.0–1.5 mm, apex acuminate, pubescent to tomentose. *Corolla*: lobes ovate or occasionally elliptic, free to the base, 4–6(–7) × 2.4–4.1 mm; inside yellow, occasionally tinted with purple or lilac, outside yellow, brown or purple, these often in combination; abaxial surface with a few sericeous hairs. *Corona lobes* produced ± 0.5 mm above corolla, cucullate-cyathiform, 4–6(–7) × 2.4–4.1 mm, upper proximal ends forming 2 rounded shoulders, occasionally extended into short pointed appendages, level with or projecting (slightly) onto style apex, distal end obtuse or rounded without a distinct appendage and level with or lower than style apex, saccate cavity with a tongue-like or deltoid-oblong appendage 0.2–0.8 mm wide, projecting 0.2–0.7 mm above upper lobe margin, colour yellow to bright yellow. *Staminal column* 2.0–2.8 mm long; anther wings shallowly concave in upper two thirds, rounded at base, 0.75–1.1 × 0.3–0.5 mm; anther appendages pescapriform or ovate with a deep apical cleft, membranous, 0.3–0.6 × 0.6–0.9 mm, decumbent on style apex. *Style apex* truncated, with thickened undulating margins, concave in centre, 1.1–2.1 mm diameter, bright green to white. *Pollinaria*: corpusculum (0.22–)0.28–0.32 × 0.08–0.16 mm; translator arms 0.2–0.32(–0.36) mm long, thin with small transparent hook-like wings, pollinia clavate, 0.68–0.80(–0.84) × 0.24–0.36 mm. *Fruits* and *seeds* not seen. *Specific epithet etymology*: from the Greek words diplo- (two) and glosso- (tongue); probably in reference to the corona lobe and the appendage in its central cavity. (Figure 2.1).

Aspidonepsis diploglossa is found in annually burnt montane grasslands, normally on south- or east-facing hillside slopes or mountain plateaux. Usually, but not always, occurring in wettish areas. Collectors often report it as rare, although a great many collections exist. It is usually found growing at altitudes ranging from 1 500 to 2 400 m, but occasionally also at lower altitudes. Plants flower from October to January. The tubers of this plant lie just below the soil surface, and when sectioned reveal white, woody flesh that oozes sticky, milky latex.

A. diploglossa, a mountain-loving species, exhibits a rather strange distribution. It may be found at high altitudes around Grahamstown and Hogsback in the eastern Cape, then there is a gap in the Transkei Drakensberg (which may be an artifact caused by poor collection in this area) and then it occurs abundantly along the Natal Drakensberg and its foothills as far as Van Reenen's Pass. After yet another gap it is found again in the Wakkerstroom area. *A. diploglossa* may also inhabit mountain islands in the Natal midlands at places such as Inanda, Greytown and Weenen. However, it occurs in the most unlikely place near the southern Natal coast at the Umtamvuna Nature Reserve, where it grows at an altitude of only 350 m. This nature reserve is well known scientifically because it lies within the narrow belt of Natal Group sandstone in the coastal region between Port Shepstone and Port St Johns. Its rich flora includes a number of rare plants and endemic species. However, the occurrence of *Aspidonepsis diploglossa* at such a low altitude and so near the sea, is surprising and inexplicable (Figure 3).

Unfortunately, when R. Schlechter described *Asclepias schizoglossoides* in 1894 he not only failed to cite the specimens he examined, but was also unaware that he was dealing with an already described taxon. Turczaninow had named this species *Gomphocarpus diploglossus* in 1848, citing *Ecklon 23* as the type. N.E. Brown picked up these two errors when preparing the Asclepiadaceae for *Flora capensis*, and in correspondence with Schlechter discovered that the latter taxonomist had based the name *Asclepias schizoglossoides* on a Barber specimen 'probably collected in British Kaffraria'. As a result, N.E. Brown (1908) suspected that the specimen may be part of Mrs Barber's gathering numbered 35. N.E. Brown's selection of *Barber 35* as the type of the name *Asclepias schizoglossoides* for *Flora capensis* was probably correct. However, due to the destruction of Schlechter's asclepiadaceous collections housed at Berlin herbarium during the Second World War, we cannot confirm this. In this paper we have, therefore, chosen *Barber 35* (K) as the neotype of the name *Asclepias schizoglossoides*.

W.H. Harvey has written (in pencil) on two Trinity College Dublin herbarium (TCD) sheets of this species, the name *Gomphocarpus luteus* (var.) β *heterophyllus*. This name was never validly published, and must be considered nothing more than a manuscript name.

Aspidonepsis diploglossa differs from *A. flava* and *A. cognata* in possessing longer (occasionally narrower) leaves, a deeply cleft anther appendage, yellow to yellow-brown flowers and a simple cup-shaped corona lobe, the upper proximal ends of which are no more than blunt rounded shoulders level with the style apex. See Table 3.

NATAL.—2730 (Vryheid): Altemooi, (–AD), *Thode A1173* (NH, PRE). 2731 (Louwsburg): near Ngome, (–CD), *Schrire 1037* (NH). 2828 (Bethlehem): Royal Natal National Park, (–DB), *Trauseld 122* (PRE); Mont Aux Sources, (–DD), *Schweickerdt 779* (PRE). 2829 (Harrismith): Van Reenen, (–AD), *Jacobsz 1656* (PRE); Klawervlei, (–CA), *Blom 287* (PRE); Cathedral Peak State Forest, (–CC), *Killick 1016* (CPF, PRE). 2830 (Dundee): Weenen, (–CC), *Rogers 28436* (K). 2929 (Underberg): Giant's Castle, (–AB), *Stewart 2070* (K, NU); Tabamhlope Mountain, (–BA), *West 1383* (NH, PRE); Highmoor State Forest, (–BC), *Killick & Vahrmeijer 3583* (K, NH, PRE); Restmount area, (–CB), *Hilliard & Burtt 15557* (K); Bushman's Nek area, (–CC), *Hilliard & Burtt 17436* (K, PRE); Garden Castle Nature Reserve, (–CD), *Hilliard & Burtt 7866* (K, NU); Runnymeade, (–DB), *Moll 1480* (NU); near Maiwaga, (–DC), *Rennie 235* (NU); Glengariff, (–DD), *Rennie 488* (NU). 2930 (Pietermaritzburg): near Pietermaritzburg, (–AC), *Ram s.n.* (NU); Caversham, (–AD), *Mogg 2471* (PRE); Greytown, (–BA), *Wylie s.n.* (K, NH 21644, PRE ex Transvaal Museum 34205); Dargle, (–CA), *Fannin 39* (K, TCD); near Richmond, (–CD), *Wood 10819* (NH); Inanda, (–DB), *Groom s.n.* (K ex Wood 1408, NH 4106).

TRANSKEI.—3028 (Matatiele): near Ramatseliso, (–BB), *Boardman A11* (PRE). 3029 (Kokstad): Ensikeni, (–BA), *Haygarth s.n.* (NH ex Wood 12049). 3130 (Port Edward): Umtamvuna Nature Reserve, (–AA), *Abbott 2868* (NH).

CAPE.—3227 (Stutterheim): near Fort Cunynghame, (–AD), *Sim s.n.* (BOL); Hogsback, (–CA), *Rattray s.n.* (BOL 15767); Dohne Hill, (–CB), *Sim 1237* (BOL, NU, PRE, SAM). 3326 (Grahamstown): Coldspring, (–AD), *Glass 276* (K, PRE, SAM); Howison's Poort, (–AD), *Hutton s.n.* (TCD); Grahamstown, (–BC), *MacOwan 850* (K).

WITHOUT PRECISE LOCALITY.—Eastern Cape, *Barber 35, s.n.* (K); Cape, (Mrs Barber records it as being collected at the Winterberg, but its occurrence there is highly improbable. Possibly she meant the Winterhoek Mountains near Uitenhage or the Klein Winterhoek near the Zuurberg, where its occurrence is much more likely) *Barber 84* (K, TCD).

2. **Aspidonepsis flava** *(N.E. Br.) A. Nicholas & D.J. Goyder*, comb. nov. Type: Transkei, Malowe Mountain, *Tyson 1086* (K! lecto., here designated; BOL!, SAM!, isolecto.)

Asclepias flava N.E. Br.: 687 (1908); Wood: 460 (1910).

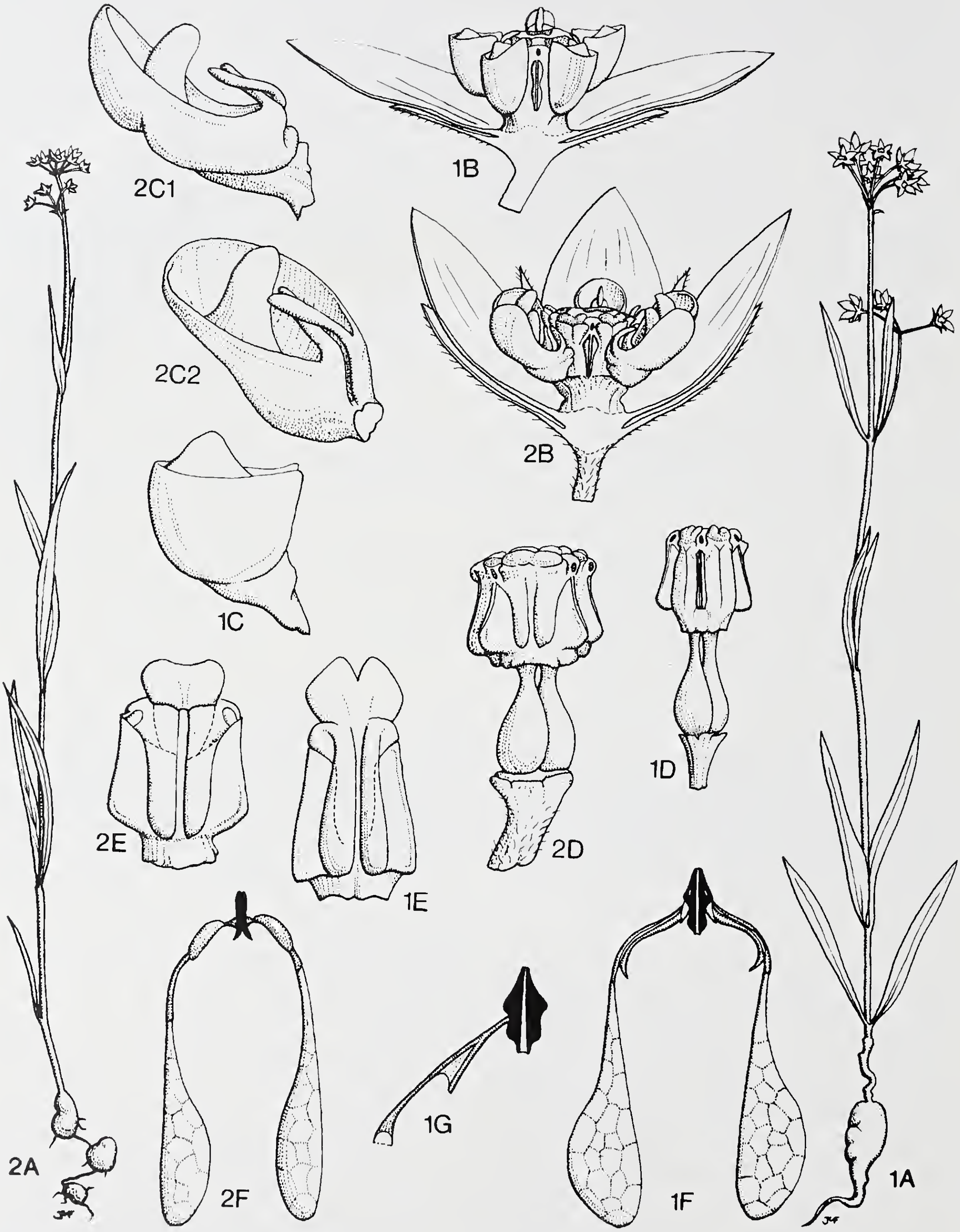

FIGURE 2.—1, *Aspidonepsis diploglossa*; 2, *A. flava*. A, whole plant with flowers: 1A, × 0.7; 2A, × 0.4. B, flower with part of corolla removed: 1B, × 10; 2B, × 9. C, corona lobe: 1C & 2C1, side view, × 14 & × 27; 2C2, angled view to show crossed, inwardly flexed proximal appendages, × 30. D, gynostegium excluding corona: 1D, × 16; 2D, × 19. E, abaxial surface of anther: 1E, × 24; 2E, × 30. F, pollinarium: 1F, × 51; 2F, × 65. 1G, translator apparatus showing winged spur, × 89. 1A, *Ruddock 136* (CPF); 1B, 1D, 1E, 1F, *Boardman All* (PRE); 1C, 1G, *Boardman 186* (PRE); 2A–2C1, 2D–2F, *Coleman 813* (PRE); 2C2, *Wood 4249* (NH).

TABLE 3.—A comparison of the three species of subgenus *Aspidonepsis*. All measurements in mm

Character	*A. diploglossa*	*A. flava*	*A. cognata*
Leaf length	5–33	7–83	7–68
Petiole length	0–4	0–5	0–3
Peduncle length	0–95	4–175	3–92
Flower colour	Yellow purple	Yellow, yellow & brown	Yellow-green
‡ Petal length	4–7	3.5–5.0	5.8–10.5
* Corona lobe shape	Bonnet-like	Cup-like	Bowl-like
* Coronal lobe cavity depth	1.1–2.0	0.4–0.7	2.2–2.5
# Proximal corona lobe appendage length	None	0.25–0.7	0.6–1.2
+ Corona lobe cavity appendage length	0.2–0.7	0.4–0.7	0.8–1.3
● Alar fissure length	0.75–1.1	0.5–0.7	0.8–1.4
‡ Anther appendage length	0.6–0.9	0.5–0.8	0.8–1.3
Style apex diameter	1.1–2.1	1.1–1.6	1.5–2.8
● Pollinium length	0.68–0.84	0.48–0.68	0.72–0.96
● Pollinium width	0.24–0.36	0.16–0.24	0.24–0.32

Discontinuities between *A. diploglossa* and the other two taxa; ● discontinuities between *A. flava* and the other two taxa; + discontinuities between *A. cognata* and the other two taxa; ‡ discontinuities between *A. flava* and *A. cognata*; * discontinuities between all three taxa.

Rootstock a globose tuber, occasionally several connected in series, 6–10 × 4–9 mm. *Stems* usually 1, rarely as many as 3, slender, erect, 180–475 mm long. *Leaves* spreading to erect, lanceolate, linear to narrow-elliptic, 7–83 × 0.5–6.0(–7.0) mm; apex acuminate or rarely acute; base petiolate to cuneate. *Inflorescences* 1–3(–6) per plant, 1–3 per stem, 4–18(–24)-flowered; bracts present at anthesis, 2.6–5.3(–7.5) × 0.15–0.5 mm; peduncles (4–)10–175 mm long. *Flowers* 3–5(–6) × 5–8 mm; pedicel 5–11 mm long. *Calyx*: lobes lanceolate, 2.0–3.6(–4.0) × 0.7–1.2 mm. *Corolla*: lobes ovate, occasionally elliptic, free to the base, 3.5–5.0 × 2.0–3.2 mm, inside greenish yellow or yellow, outside yellowish green, pale yellow or yellow with a purple apex, margins occasionally slightly revolute. *Corona lobes* produced 0.5–0.8 mm above corolla, cucullate-crateriform, in side view boxing glove-shaped, 1.0–1.6 mm long, upper proximal ends extending into 2 short (0.25–0.70 mm), subulate or arm-like appendages that meet and are then reflexed back to point to distal end of lobe, lower than style apex, distal end dilated and bowl-shaped with upper margin overtopping the style apex (even if only slightly); cavity crateriform, 0.4–0.7 mm deep with a central sausage-shaped appendage projecting 0.4–0.7 mm above cavity margin; orange-yellow, golden yellow, yellow-green or yellow. *Staminal column* 1.0–1.5 mm long; anther wings shallowly concave in upper two thirds, rounded in lower third, truncate basally, 0.5–0.7 × 0.2–0.45 mm; anther appendages reniform, membranous, (0.2–)0.3–0.4 (–0.5) × 0.5–0.8 mm, decumbent on sides and top of style apex. *Style apex* truncate, margin undulate, apex concave with a small central pore, 1.1–1.6 mm wide. *Pollinaria*: corpusculum 0.16–0.20(–0.26) × (0.60–)0.08–0.10 mm; translator arms (0.20–)0.18–0.28 mm long; pollinia dilated distally, narrowing proximally, (0.48–)0.52–0.64 (–0.68) × 0.16–0.24 mm. *Fruits*: mature follicles not seen, immature follicles narrowly fusiform with an attenuate apex, not echinate. *Seeds* not seen. *Specific epithet etymology*: from the Latin word *flav(us)* meaning pale yellow. This is in reference to the pale yellow flowers of this species. (Figure 2.2).

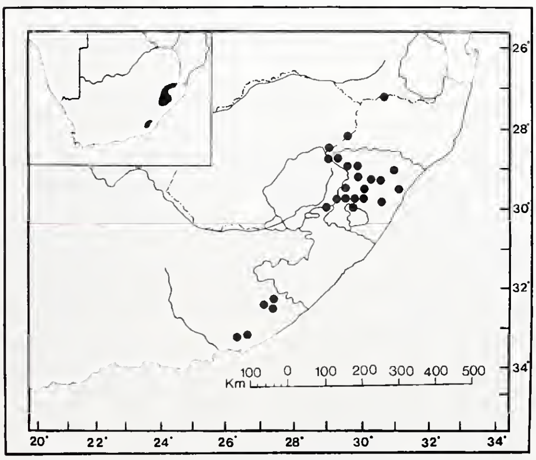

FIGURE 3.—Distribution of *Aspidonepsis diploglossa*.

Aspidonepsis flava is usually found growing in annually burnt montane grasslands. Colonies are usually scattered and occur at altitudes between 600 and 2 000 m, rarely at altitudes as low as 450 m. Distributed from Grahamstown in the eastern Cape through Transkei to Natal. This species is commonly found in the Drakensberg or its foothills, although it can be found in the midland and coastal belts if mountainous areas provide it with a suitable refuge (Figure 4). *A. flava* flowers in the midsummer months between November and January, although there is one record of a plant flowering in October.

This taxon was first described by N.E. Brown in *Flora capensis* (1908), and is abundant in southern Natal and the Transkei interior. The limits of its southern distribution is near Grahamstown where a few specimens have been collected. Plants grow in small colonies in annually burnt grasslands, and usually occur on hillside slopes amongst scattered rocks where they receive some protection from grazing animals and fire. Plants may have up to three tubers connected in series, each probably representing a previous year's growth. Like *A. diploglossa*

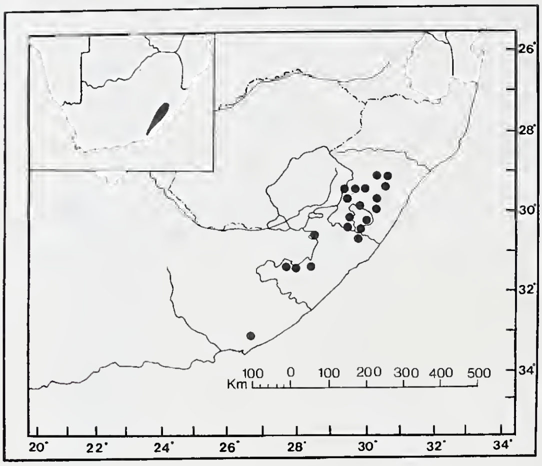

FIGURE 4.—Distribution of *Aspidonepsis flava*.

these globose tubers are found just below the soil surface, and have white, latex-filled flesh.

A. flava is distinguished from the other two species in subgenus *Aspidonepsis* by its longer peduncles, smaller, paler coloured flowers, smaller pollinaria, bowl-shaped corona lobes with arm-like proximal appendages that cross one another and are then reflexed into the corona lobe cavity and the sausage-shaped appendage projecting from the floor of the corona lobe cavity. Table 3.

NATAL.—2929 (Underberg): Cobham State Forest, (—CB), *Cowan 124* (NU); near Underberg, (—CD), *Dyer 3744* (K, NH); Mawahqua Mtn area, (—DA), *Rennie 275* (NU); Mpendle, (—DB), *Huntley 625* (NH); Nkonzo State Forest, (—DD), *Nicholas & Norris 1159* (CPF, NH, PRE). 2930 (Pietermaritzburg): Howick, (—AC), *Hutton 408* (BM, K, PRE); Benvie, Karkloof, (—AD), *Hilliard & Burtt 13491* (NU); Winterskloof, (—CB), *Sim s.n.* (PRE); near Byrne Village, (—CC), *Stewart 2023* (K, NU); Weza State Forest, (—DA), *Nicholas 2080* (NH); Fort Donald, (—DC), *Tyson 1660* (SAM). 3030 (Port Shepstone): Ixopo, (—AA), *Shirley s.n.* (NU).

TRANSKEI.—3028 (Matatiele): near Eland's Height, (—CD), *Stewart 1908* (NU). 3029 (Kokstad): near Mt Currie, (—AD), *Hutchinson 1823* (K), *Tyson 1686* (BOL, PRE, SAM); Ensikeni, (—BA), *Haygarth s.n. ex Wood 12049* (NH 18644, SAM); Malowe, (—BD), *Tyson 2723* (K, SAM); Vaal Bank, (—CB), *Haygarth s.n. ex Wood 4230* (K, NH). 3127 (Lady Frere): Mount Kwenkwe, (—DA), *Bolus 10215* (BOL), Engcobo, (—DB), *Bolus 10216* (BOL). 3128 (Umtata): Mhlahlane, (—BC), *Hutchings 1387* (KEI); Bazija, (—CB), *Baur 556* (K, SAM).

CAPE.—3326 (Grahamstown): Grahamstown, (—BC), *Glass 1503* (K, NBG).

WITHOUT PRECISE LOCALITY.—Natal (Liddesdale), *Wood 4249* (K, NH); *Gerrard 1315* (BM, K).

3. **Aspidonepsis cognata** *(N.E. Br.) A. Nicholas & D.J. Goyder*, comb. nov. Type: Transkei, Mount Insizwa, *Schlechter 6496* (K!, holo.; BOL!, NH!, PRE!, iso.)

Asclepias cognata N.E. Br.: 687 (1908).

Rootstock a tuber, ± 7×7 mm. *Stems* 1, erect, 180–550 mm tall. *Leaves* spreading to ascending, linear, occasionally lanceolate, (7–)11–68 × (0.3–)0.7–4.0(–6.0) mm; apex acuminate, base shortly petiolate, occasionally cuneate. *Inflorescences* occasionally subtended by leaves, 1–2 per plant, 1–7(–9)-flowered; bracts not fugaceous, grading with leaves; peduncles 3–76(–92) mm long. *Flowers* 5–12 × 7–17 mm; pedicels 6–12 mm long. *Calyx*: lobes lanceolate, 3.0–5.0 × 1.0–1.8 mm, apex acuminate. *Corolla* glabrous; lobes elliptic, occasionally narrow-elliptic to ovate, (5.8–)7.6–10.5 × 2.6–5.8 mm, apex acute, inside yellow, yellow-purple, brown-purple, yellow and lilac, outside pale greenish yellow sometimes suffused purple, or mustard yellow, or greenish brown, or base yellow and apex purple, or base mauve and apex yellow to dark brown, or yellow-brown with purple veins. *Corona lobes* produced 1.5–1.8 mm above corolla, cucullate, bonnet-shaped, 3.0–4.8(–5.3) [oblique measurement] × 1.3–2.5 mm, upper proximal ends extended into 2 short (0.6–)0.8–1.2 mm, subulate or arm-like appendages sometimes projecting over style apex, dilated distal end overtopping style apex by 0.6–1.0 mm and truncated along its upper margin; cavity 0.8–1.3 mm deep with a yellow tongue-like central appendage projecting 0.8–1.3 mm above lip of corona lobe (i.e. almost level with the upper margin of the distal end); colour dull yellow-green, mustard yellow, or yellow and purple, with red or brown along the margin. *Staminal column* 1.5–2.6 mm long; anther wings 0.8–1.4 × 0.4–0.6 mm; anther appendages reniform, membranous, 0.3–0.6 × 0.8–1.3 mm, decumbent on the sides of the style head. *Style apex* truncated with thickened undulate margins, concave with a small pore in the centre, 1.5–2.8 mm wide. *Pollinaria*: corpusculum 0.2–0.3 × 0.1–0.12 mm; translator arms 0.32–0.56 mm long; pollinia semi-circular to semi-ovate with a short narrow proximal end, 0.72–0.96 × 0.24–0.32 mm. *Fruits*: mature follicles not seen, young follicles tomentose (but not echinate). *Seeds* not seen. *Specific epithet etymology*: from the Latin word *cognat(us)* meaning related. Unfortunately, N.E. Brown did not explain the sense in which he applied this name. (Figure 5).

Aspidonepsis cognata may be found scattered in annually burnt (but not always) montane grassland, usually occurring in river valleys or near streams where the soil is quite damp. This graceful species flowers between November and December (although there is one record for October), and occurs at altitudes between 1 200 and 2 100 m, rarely lower. *A. cognata* is confined to a small area in the southern Natal and northern Transkei Drakensberg (Figure 6).

It is unfortunate that N.E. Brown (1908) chose *Schlechter 6469* as the type of *Asclepias cognata*, because this collection is not typical of the species as a whole. However, all specimens of *Schlechter 6469* examined, although not typical, clearly belong to this species. In appearance *Hilliard & Burtt 7855* is more representative of the species.

Aspidonepsis cognata can be distinguished from the other species in subgenus *Aspidonepsis* by its larger flowers, larger corona lobes which are broadly helmet-shaped, wider anther appendages and its longer translator arms and pollinia. (See Table 3). The corona lobe shape is highly diagnostic, in particular the subulate or arm-like proximal appendages which may project over the style apex, and the raised distal end which is usually truncated along its upper margin and overtops the style head.

NATAL.—2929 (Underberg): Fort Nottingham Commonage, (—BD), *Wright 2241* (NU); Gxalingenwa Valley, (—CB), *Hilliard & Burtt 17090* (K, PRE); Garden Castle State Forest, (—CC), *Hilliard & Burtt 13767* (K, NU); Umzimkulu headwaters, (—CD), *Hilliard & Burtt 7855* (K, NU); Mpendle, (—DB), *Hilliard & Burtt 13856* (NU).

TRANSKEI.—3029 (Kokstad): Ensikeni, (—BA), *Haygarth s.n. ex Wood 12045* (K, NH 13661); Mount Insizwa, (—CD), *Schlechter 6496*

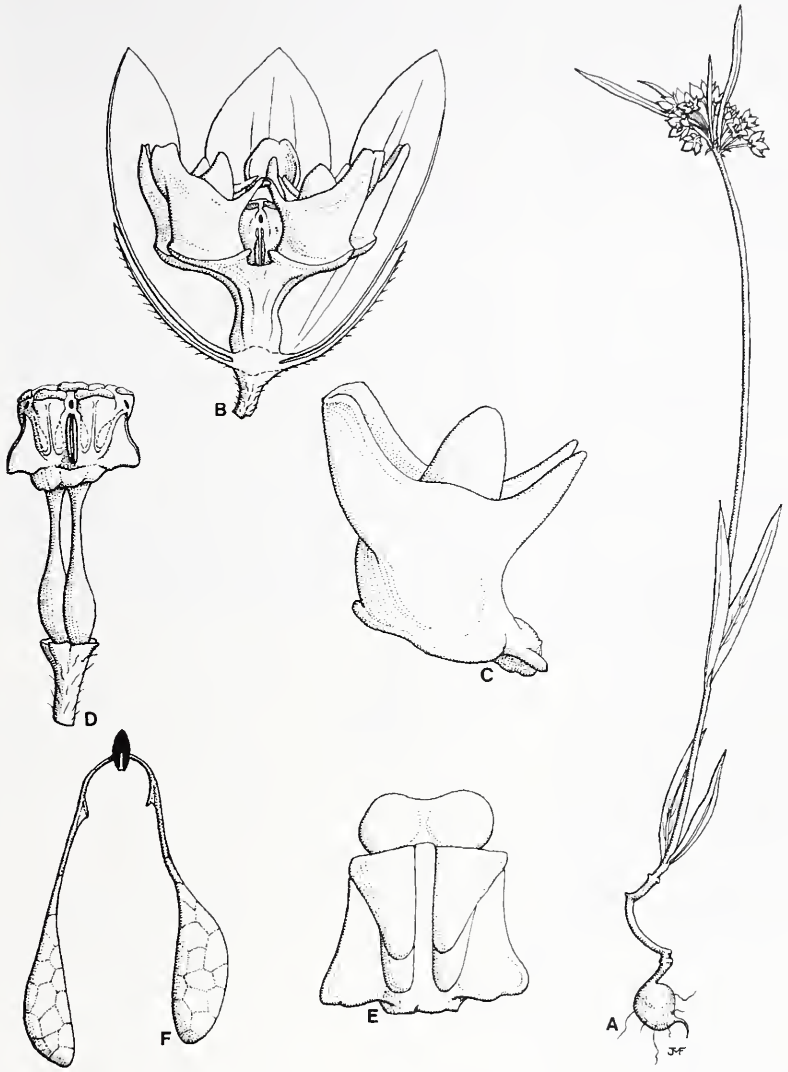

FIGURE 5.—*Aspidonepsis cognata*. A, whole plant with flowers, × 0.5; B, flower with part of corolla removed, × 4.5; C, corona lobe side view, × 11; D, gynostegium excluding corona, × 9; E, abaxial surface of anther, × 19.5; F, pollinarium, × 36. A–F, *Hilliard & Burtt 9056* (NU).

(BOL, K, NH, PRE); Weza State Forest, (–DA), *Nicholas 2081* (NH, MO).

B. Subgenus **Unguilobium**

Unguilobium *A. Nicholas & D.J. Goyder*, subgen. nov.

Folia ascendentia, margine manifeste revoluta. *Inflorescentia* 4–11-flora. *Corolla* reflexa; pagina abaxialis pubescentia. *Coronae lobi* ad columnam staminalem circa 1 mm super insertionem corollae conjuncti, cucullati; appendix proximalis ad apicem deltato-falcata et apicem styli aequans vel superans impendensque; extremum distale coronae appendice parva ornatum (*A. reenensis*) vel appendice carente (*A. shebae*); sinus profundus rimiformis.

TYPUS.—*Aspidonepsis reenensis* (N.E. Br.) A. Nicholas & D.J. Goyder *vide infra*.

Stems 1, erect, thin, up to 625 mm tall. *Leaves* ascending, linear, occasionally lanceolate, older leaves shorter and broader, margins noticeably revolute. *Inflorescences* 4–11-flowered, bracts present at anthesis and grading in size and shape with leaf system. *Flowers* purple, brown, lilac and yellow. *Corolla* reflexed, lobe apices ascending, abaxial surface pubescent. *Corona* produced high on staminal column, ± 1 mm above corolla; lobes with proximal appendages deltoid-falcate with obtuse apex level with or projecting over style apex, distal end of corona with arm-like appendage reflexed into corona lobe cavity (*A. reenensis*) or without appendage (*A. shebae*). *Staminal column*: anther wings ear-like in outline; anther appendages pescapriform, deeply cleft at apex (*A. shebae*), or ovate to rectangular and occasionally cleft at apex (*A. reenensis*). *Style apex* with slightly thickened, undulate margins. *Pollinia*: distal end noticeably dilated and narrowed towards proximal end. *Etymology*: from the Latin words *ungu(is)* (claw) and *lob(us)* lobe, in reference to the claw-shaped corona lobes of this subgenus (Table 2).

There are two species in subgenus *Unguilobium*, viz. *A. reenensis* (the type species) and *A. shebae*. Both are

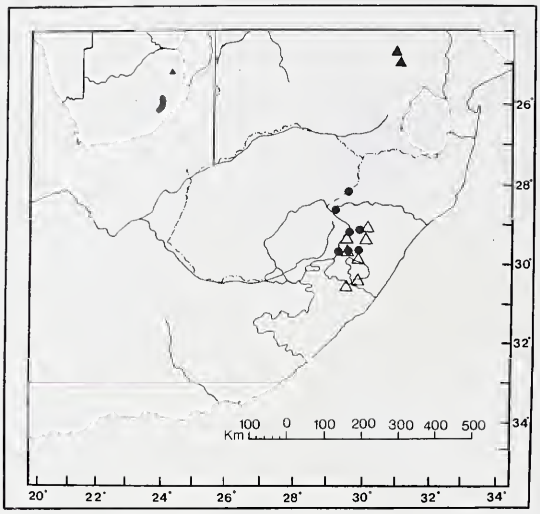

FIGURE 6.—Distribution of *Aspidonepsis cognata*, △; *A. reenensis*, ●; and *A. shebae*, ▲.

confined to mountainous areas of the southern African Drakensberg. *A. reenensis* is found in the southern regions of this mountain system (namely Natal), whereas *A. shebae* is found in the northeastern region (the eastern Transvaal). As such, these species are quite widely separated geographically (Figure 6). Although probably related (even if somewhat distantly), they can be easily told apart using corona lobe and anther appendage shape.

4. **Aspidonepsis reenensis** *(N.E. Br.) A. Nicholas & D.J. Goyder*, comb. nov. Type: South Africa, Natal, Van Reenen, *Wood 8635* (K! holo.; GRA!, NH!, PRE!, SAM!, iso.).

Rootstock a tuber, 17–25(–41) × 7–14 mm. *Stems* 1, erect, 240–520(–625) mm long, scabrous. *Leaves* linear, 10.0–56.0 × 0.7–2.5(–4.0) mm, apex acuminate, base cuneate; usually apetiolate or petiole up to 1 mm long. *Inflorescences* occasionally a number massed towards the stem apex, 1–3(–4) per plant, (1–)4–8-flowered; bracts 2.50–5.90 × 0.25–0.50 mm; peduncles (9–)12–65(–75) mm long. *Flowers* (4–)5–7 × 7–11 mm; pedicel 9–15 (–21) mm long. *Calyx* reflexed, lobes lanceolate, apex acuminate, 2.7–4.5 × 1.0–1.7(–2.5) mm. *Corolla*: lobes narrow-elliptic to ovate, 5.5–6.5 × 2.5–3.8 mm, colour (inside and out) dark reddish brown, dark brown, brown, dull reddish purple or purple, margins light yellow or

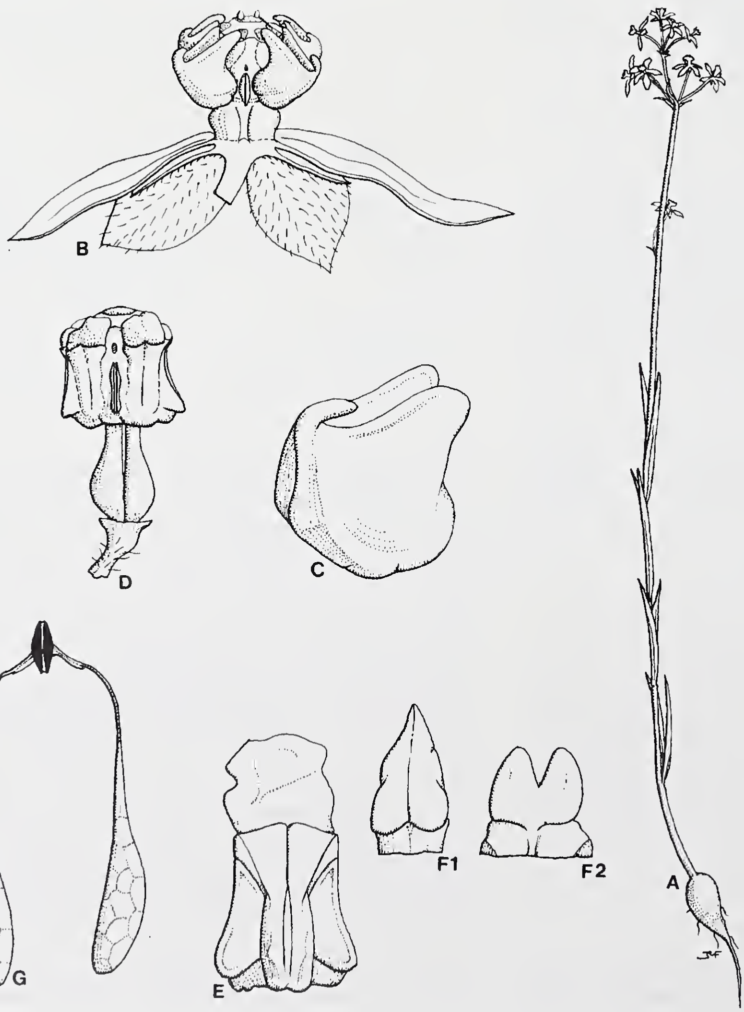

FIGURE 7.—*Aspidonepsis reenensis*. A, whole plant with flowers, × 0.4; B, flower with part of corolla removed, × 7; C, corona lobe, side view, × 12; D, gynostegium excluding corona, × 8.5; E, anther, × 27. F, anther appendage: F1, uncleft, × 12; F2, cleft, × 12; G, pollinarium, × 40. A–E, F2, G, *Killick 1205* (PRE); F1, *Trauseld 1042* (PRE).

purple to white, abaxial surface puberulent to villous, especially in centre and towards the base. *Corona lobes* produced from staminal column 0.8–1.0 mm above corolla, cucullate, almost cyathiform, (1.6–)2.2–2.6 × 1.3–1.8 mm; upper proximal ends forming 2 short, falcate, arm-like appendages with rounded or broad and frilly apices, (0.4–)0.7–1.3 × 0.4–1.0 mm, projecting over or (at least) raised above the style apex; distal appendage short (± 0.5 mm), broad and arm-like, reflexed into the cavity (sometimes totally hidden by sides of lobe), appendage below style apex and almost level with corpusculum. *Staminal column* ± 3 mm tall, slightly inflated in lower portion below each corona lobe; anther wings shaped like an elongated ear lobe, 0.8–1.1 × (0.3–)0.4–0.5 mm; anther appendages ovate to rectangular, appearing wrinkled, white, membranous, occasionally cleft at apex, 0.8–1.5 × 1.0–1.3 mm, decumbent on style apex. *Style apex* truncate with undulate margins, concave with a small central pore, 1.8–2.4 mm wide. *Pollinarium*: corpusculum 0.28–0.34 (–0.40) × 0.12–0.18 mm; translator arms 0.44– 0.64 mm long, thin, transparent; pollinia dilated distally with a long narrow proximal arm-like section, 0.84–1.00 × 0.22–0.28 mm. *Fruits* and *seed* not seen. *Specific epithet etymology*: a latinization of Reenen from Van Reenen's Pass, the type locality of this species (Figure 7).

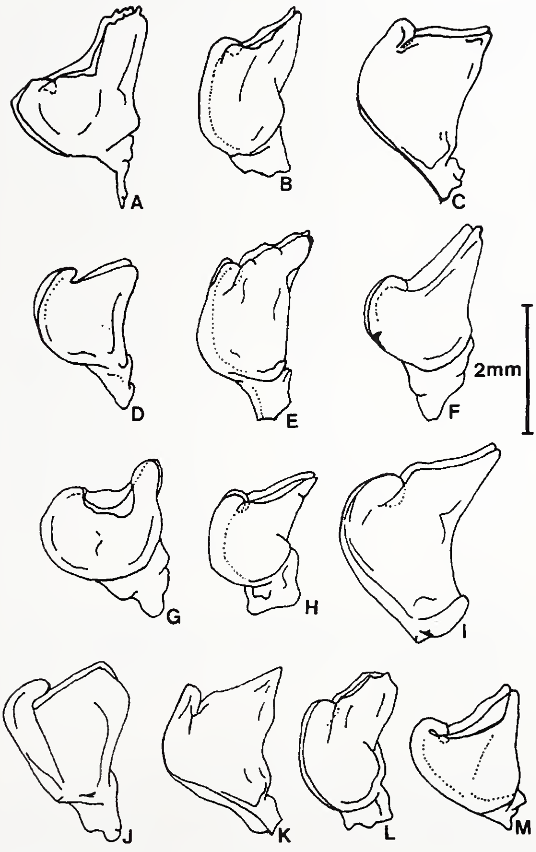

FIGURE 8.—Corona lobe variation in *Aspidonepsis reenensis*. A, *Wood 8635* (PRE); B, *Stewart 2110* (NU); C, *Hilliard & Burtt 7796* (NU); D, *Killick & Vahrmeijer 3654* (PRE); E, *Hilliard & Burtt 9423* (NU); F, *Killick 1205* (NU); G, *Franks s.n. (NH 12112)*; H, *Hilliard & Burtt 9481* (NU); I, *Wood 8635* (NH); J, *Trauseld 1042* (PRE); K, *Hilliard & Burtt 7796* (NU); L, *Rennie 1109* (NU); M, *Wood 8635* (SAM).

A. reenensis grows in dry mountain grasslands, often in sandy situations on top of the Cave Sandstone zone of the Little Berg. It also occurs in *Themeda triandra* veld, which is indicative of a fire climax community (Killick 1963). This species, said by collectors to be frequent to rare, is found in the Natal Drakensberg, from Bushman's Nek in the south to Van Reenen's Pass in the north (Figure 6). It occurs at altitudes varying from 1 500 to 2 100 m, and flowers in the midsummer months, December and January, with one record from November.

Corona lobe structure in the tribe Asclepiadeae is very species-specific and usually uniform within a species (Nicholas 1987). There are however certain exceptions, *A. reenensis* being one of them. The corona lobe structure of this species is extremely variable, although one can still see an underlying, and therefore unifying, corona lobe pattern (Figure 8).

NATAL.—2829: (Harrismith): Van Reenen, (–AD), *Franks s.n. ex Wood 12112* (NH); *Hilliard & Burtt 9481* (NU); *Wood 8635* (GRA, K, NH, PRE, SAM); Mount Manyanyeza, (–AD), *Stewart 2110* (NU); Cathedral Peak State Forest, (–CC), *Killick 1205* (CPF, K, NH, PRE). 2929 (Underberg): Giant's Castle Nature Reserve, (–AD), *Trauseld 1042* (PRE); Highmoor State Forest, (–BC), *Killick & Vahrmeijer 3654* (K, PRE); Cobham State Forest, (–CC), *Hilliard & Burtt 9423* (NU); Garden Castle State Forest, (–CD), *Hilliard & Burtt 7796* (NU); Mawahqua Mtn area, (–DC), *Rennie 1109* (NU).

5. **Aspidonepsis shebae** *A. Nicholas & D.J. Goyder*, sp. nov., *A. reenensi* (N.E. Br.) A. Nicholas et D.J. Goyder affinis sed coronae lobis unguiformibus nec cyathiformibus, appendice proximali brevi falcataque nec rotundata vel fimbriata, appendice distali brachiformi carente differt.

TYPE.—Transvaal, 2430 (Pilgrims Rest): (–DC), Mt Sheba Nature Reserve, *Forrester & Gooyer 216* (PRE!, holo.).

Rootstock a tuber, ± 15 × ± 7 mm. *Stems* 1, erect, 190–340 mm long. *Leaves* linear or occasionally lanceolate, 7–44 × 1–4 mm, older leaves smaller and broader, apex acuminate; usually apetiolate, rarely with petiole up to 0.5 mm long. *Inflorescence* 1–2 per plant, (2–)4–11-flowered; peduncle (5–)19–90 mm long. *Flowers* 4.0–6.5 × 6.0–8.0 mm; pedicel 10–15 mm long. *Calyx*: lobes lanceolate, 3.4–3.6 × 1.1–1.3 mm. *Corolla*: lobes ovate or rarely elliptic, 5.1–5.8 × 3.0–3.6 mm; inside: base pale yellow with a lilac apex, or base lilac with a dark purple apex; outside: base green-yellow with a purple or dark purple apex; margins pale yellow to white; abaxial surface pubescent. *Corona lobes* produced from staminal column ± 1 mm above corolla, claw-like (unguiform), 1.8–3.0 × 2.0–2.1 mm; upper proximal ends extended into 2 short, falcate, subulate appendages projecting over style apex; distal end a square, blunt shoulder which is ± level with style apex; cavity a shallow, central channel ± 0.9 mm deep; yellow in dried specimens. *Staminal column* ± 2.5 mm tall; anther wings ear-shaped, ± 0.7 × 0.4–0.45 mm; anther appendages pescapriform, deeply cleft at apex, membranous, ± 0.5 × ± 0.7 mm, decumbent on style apex. *Gynoecium*: style apex truncate, concave with a small central pore, 1.6–1.8 mm wide; ovaries noticeably pubescent. *Pollinarium*: corpusculum 0.20–0.26 × 0.10–0.12 mm; translator arms 0.28–0.40 mm long; pollinia

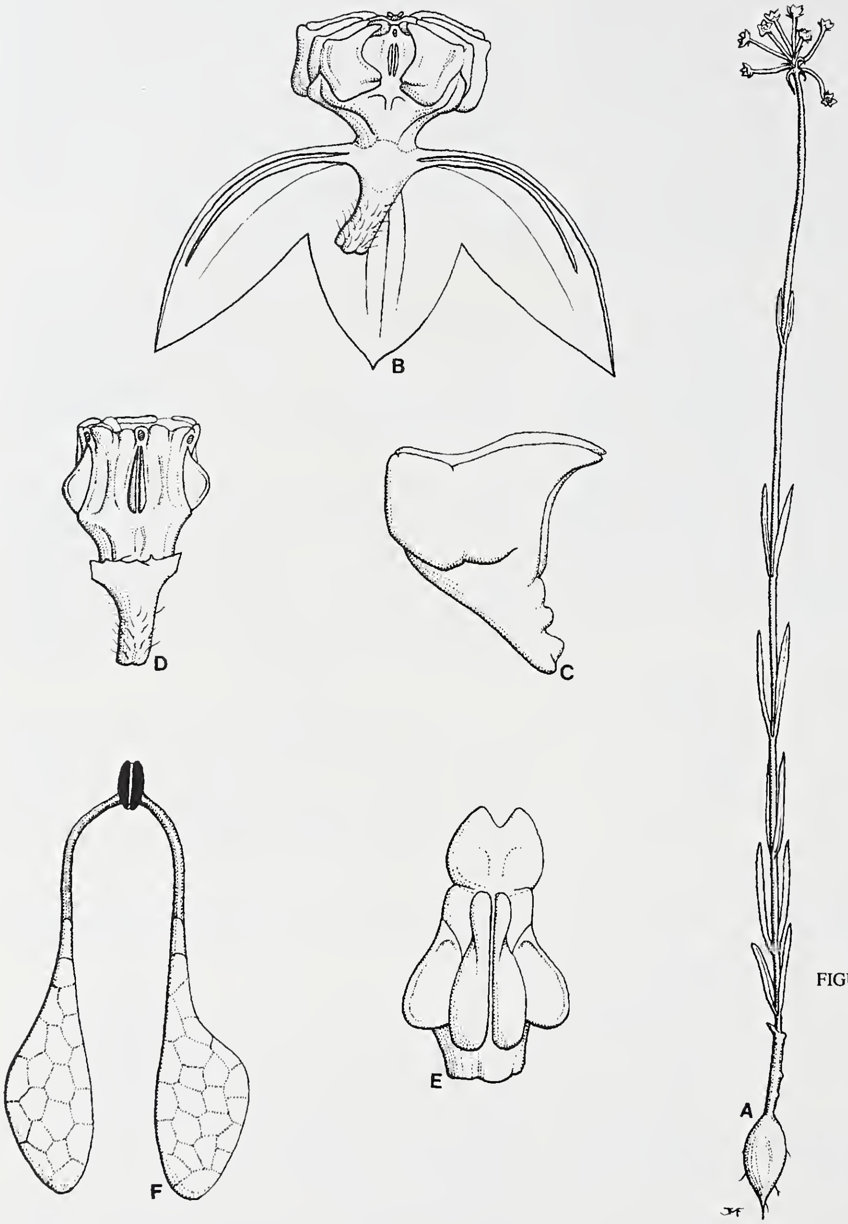

FIGURE 9.—*Aspidonepsis shebae*. A, whole plant with flowers, × 0.5; B, flower with part of corolla removed, × 7.5; C, corona lobe, side view, × 14; D, gynostegium excluding corona, × 11; E, abaxial surface of anther, × 24; F, pollinarium, × 53. A, B, D–F, *Smuts & Gillett 2326* (PRE); C, *Forrester & Gooyer 216* (PRE).

clavate, 0.68–0.76 × 0.32–0.36 mm. *Fruits* and *seeds* not seen. *Specific epithet etymology*: a latinization of Sheba from Mt Sheba, the type locality. (Figure 9).

A. shebae probably occurs in montane grasslands, and is restricted to high altitude areas (1 400 to 2 100 m) of the Pilgrim's Rest region of the eastern Transvaal (Figure 6). Plants flower in December-January, and according to one set of collections is said to be frequent.

Vegetatively *A. shebae* is very similar to *A. reenensis*, and it is probably closely related to this species (Table 4). In floral morphology, however, these two species differ greatly, especially in corona lobe structure (Figure 10).

TRANSVAAL.—2430 (Pilgrim's Rest): Mt Sheba Nature Reserve, (–DC), *Forrester & Gooyer 216* (PRE); Mauchsberg, (–DC), *Smuts & Gillett 2326* (PRE). 2530 (Lydenburg): Mount Anderson, (–BA), *Smuts & Gillett 2370* (PRE).

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TABLE 4.—A comparison of the two species in subgenus *Unguilobium*. All measurements in mm

Character	*A. reenensis*	*A. shebae*
Stem length	24.0–62.5	19–34
Leaf length	10–56	7–44
Peduncle length	9–79	5–90
Flower colour	Brown & purple	Brown, purple & yellow
Petal length	5.5–6.5	5.2–5.8
* Corona lobe width	1.3–1.8	2.0–2.1
Proximal corona lobe appendage length	0.4–1.3	± 0.5
* Distal corona lobe appendage length	± 0.5	None
* Alar fissure length	0.8–1.1	± 0.7
* Anther appendage length	0.8–1.5	± 0.5
* Anther appendage width	1.0–1.3	± 0.7
* Style apex diameter	1.8–2.4	1.6–1.8
* Translator arm length	0.44–0.64	0.28–0.4
* Corpusculum length	0.28–0.4	0.2–0.26
* Pollinium length	0.84–1.0	0.68–0.76
* Pollinium width	0.22–0.28	0.32–0.36

* characters forming discontinuities between the two taxa.

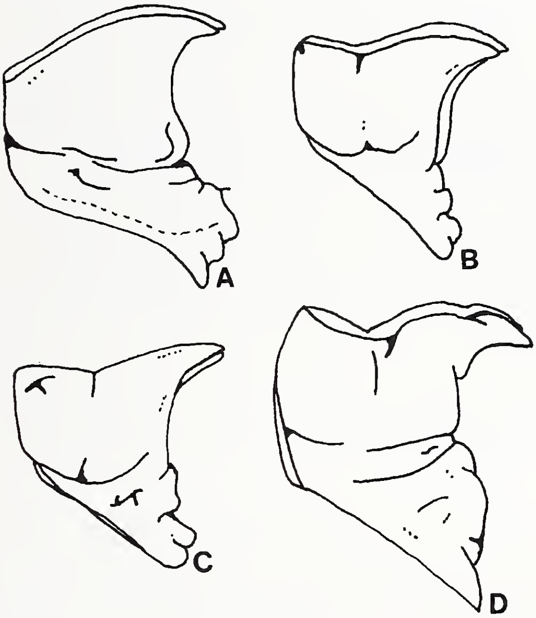

FIGURE 10.—Corona lobe variation in *Aspidonepsis shebae*. A, *Forrester & Gooyer 216* (PRE), × 16; B, *Smuts & Gillett 2326* (PRE), × 15; C, *Smuts & Gillett 2326* (PRE), × 15; D, *Smuts & Gillett 2370* (PRE), × 18.5.

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Notes on African plants

VARIOUS AUTHORS

BRYOPHYTA

NEW AND INTERESTING RECORDS OF MOSSES IN THE *FLORA OF SOUTHERN AFRICA* AREA: 2. GIGASPERMACEAE–BARTRAMIACEAE

New records identified from geographical regions referred to in the 2nd fascicle of the moss *Flora of southern Africa* (Magill 1987) are reported here. The records are listed in the same taxonomic order as in the 2nd fascicle of the moss flora and in the same format as in the first paper in the series (Van Rooy & Perold 1990).

GIGASPERMACEAE
Gigaspermum repens *(Hook.) Lindb. in Öfvers.* (Magill 1987: 299)
Southern Cape (3421 AB: *Van Zanten et al. 7608363*).

FUNARIACEAE
Goniomitrium africanum *(C. Müll.) Broth.* (Magill 1987: 313)
Western Transvaal (2526 CA: *Van Rooy 680*).
Physcomitrium spathulatum *(Hornsch.) C. Müll.* (Magill 1987: 318)
Northern Transvaal (2329 DD: *Brenan M3267*) and eastern Transvaal (2430 DB: *Vorster 649, 1553*).
Funaria
bergiana *(Hornsch.) Broth.* (Magill 1987: 323)
Lesotho (2928 BD: *Van Rooy 3180, 3183, 3205.* 2929 AC: *Van Rooy 3260, 3289, 3343, 3369.* 2929 CB: *Van Rooy 3564*), central Cape (3224 BC: *MacLea sub Rehmann 523, 523B*) and the eastern Cape (3027 CB: *Van Rooy 2703*).
urceolata *(Mitt.) Magill* (Magill 1987: 326)
Orange Free State (3026 BB: *Van Rooy 2456*) and the eastern Cape (3027 CC: *Van Rooy 2662*).
spathulata *Schimp. ex C. Müll.* (Magill 1987: 329)
Eastern Cape (3027 CA: *Van Rooy 2633.* 3027 CB: *Van Rooy 2690.* 3027 DC: *Van Rooy 2760*).

BRYACEAE
Orthodontium lineare *Schwaegr.* (Magill 1987: 336)
Southern Cape (3322 CD: *Van Zanten et al. 7609412a*).
Mielichhoferia bryoides *(Harv.) Wijk & Marg.* (Magill 1987: 338)
Central Cape (3124 DB: *MacLea sub Rehmann 548.* 3224 AD: *MacLea sub Rehmann 543b*).
Brachymenium
acuminatum *Harv. in Hook.* (Magill 1987: 343)
Eastern Cape (3027 CB: *Van Rooy 2714*).
pulchrum *Hook.* (Magill 1987: 345)
Southwestern Cape (3318 CD: *Stephens PRE-CH10132*).
Pohlia
baronii *Wijk & Marg.* (Magill 1987: 349)
Northern Transvaal (2329 BB: *Hardy 5268.* 2329 DD: *Brenan M3246*).
elongata *Hedw.* (Magill 1987: 351)
Southern Transvaal (2627 BB: *Moss PRE-CH9775*).
nutans *(Hedw.) Lindb.* (Magill 1987: 353)
Northwestern Cape (3017 BB: *Van der Westhuizen & Deetlefs 44*).
Leptobryum pyriforme *(Hedw.) Wils.* (Magill 1987: 357)
Central Transvaal, cultivated in a hothouse (2528 CA: *Clarke PRE-CH13558*) and Lesotho (2828 DC: *Deall & Killick 81*).
Bryum
nitens *Hook.* (Magill 1987: 371)
Orange Free State (2827 DD: *Perold 1311*).
capillare *Hedw.* (Magill 1987: 372)
Orange Free State (2729 AC: *Perold 1247, 1248*).
torquescens *Bruch ex De Not.* (Magill 1987: 373)
Lesotho (2928 BB: *Van Rooy 3221.* 2929 AC: *Van Rooy 3318*).
pseudotriquetrum *(Hedw.) G.M.S.* (Magill 1987: 378)
Northern Transvaal (2329 DB: *Magill 6512.* 2329 DD: *Perold 2459*).
andicola *Hook.* (Magill 1987: 384)
Eastern Cape (3027 CD: *Van Rooy 2819*).
Rhodobryum roseum *(Hedw.) Limpr.* (Magill 1987: 389)
Lesotho (2929 AC: *Van Rooy 3280, 3286*).

BARTRAMIACEAE
Anacolia breutelii *(C. Müll.) Magill* (Magill 1987: 411)
var. breutelii
Eastern Cape (3027 CA: *Van Rooy 2640.* 3027 CD: *Van Rooy 2688, 2786, 2809, 2818.* 3027 DC: *Van Rooy 2729, 2731, 2738*).
var. squarrifolia *(Sim) Magill*
Lesotho (2929 CC: *Magill 4347*).

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J. VAN ROOY* and S.M. PEROLD*

* National Botanical Institute, Private Bag X101, Pretoria 0001.
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EUPHORBIACEAE

NOTES ON *EUPHORBIA* SPECIES FROM THE NORTHWESTERN CAPE

Preparation of an account of the Euphorbiaceae for the Cape Department of Nature Conservation project 'Flora of Namaqualand' has highlighted the chaotic taxonomy of the genus *Euphorbia* in southern Africa. The monumental publication of Alain White, R. Allen Dyer & Boyd L. Sloane (1941) provides a wealth of information in the form of illustrations, but it does little to explain the extent of variation that occurs in the field. The keys provided are often unreliable and many of the species are extremely difficult to distinguish from one another.

Over the past 30 years many new species of *Euphorbia* have been described from southern Africa. Far too narrow a species concept seems to have been applied which sometimes bears little relevance to the position in nature.

During recent investigations it was found that several recently described taxa were impossible to separate from earlier, in some cases very little-known ones. Re-collection and cultivation of some of these has allowed a more in-depth comparison with newer taxa and makes some synonymy necessary.

E. celata *R.A. Dyer* in Bothalia 11: 278 (1974). Type: *Hall 4272* (PRE, holo.).

E. miscella Leach: 341 (1984a). Type: *Leach & Williamson 16545* (NBG, holo.!; PRE, iso.!).

H. Hall collected *E. celata* at two widely separated localities: north of Vredendal and along the bank of the Groen River west of Garies, about 120 km further to the north. More recent collecting has proved it to be fairly plentiful, if localized, at both of these localities and has in addition revealed its occurrence along the Swartlintjies River some 80 km further northwards as well as near Komaggas, yet further north near Lekkersing, the type locality of *E. miscella*, and near Alexander Bay at the mouth of the Orange River. The species thus seems to be of scattered occurrence over most of the low-lying parts of Namaqualand.

Both the localities Lekkersing and Alexander Bay were mentioned by White, Dyer & Sloane (1941) and Wilman (1946) for *Euphorbia wilmaniae* Marloth. Leach (1984a) was the first to point out that this material (at least from Lekkersing) represented a quite different species to *E. wilmaniae*. However, in sorting this out, he described the new species *E. miscella*. This was unnecessary in my opinion. Leach compared the new species only to *E. namuskluftensis* Leach and no mention is made of *E. celata*.

Euphorbia celata (Figure 1) is generally an insignificant plant with only short portions of stem protruding above the soil. Plants are mostly found in very exposed places, usually on or near the summit of low hills or on small outcrops in low-lying areas. They grow in crevices in rock outcrops or in flat patches of coarse quartz, granite or shale gravel shallowly overlying bedrock.

In *E. celata* the stems may become densely tufted (as in *E. namuskluftensis*), but this is not usual and they tend rather to form small clusters connected by rhizomes to the central tuber, making subsidiary roots and tubers along the way. Plants with a neat, central, ± turnip-shaped tuber such as in Dyer (1974: fig. 2) have been dug out in several localities, but more usually excavation yields a dense mass of slender, interwoven rhizomes rooting sporadically along their length with several subsidiary tubers and it is difficult to locate the central tuber. This is as recorded by Leach for *E. miscella* (Leach 1984a: fig. 1).

In the southern part of its distribution range (north of Vredendal and along the Groen River) *E. celata* has relatively few tubercles on the stems and they are essentially arranged into three angles. Along the Swartlintjies River,

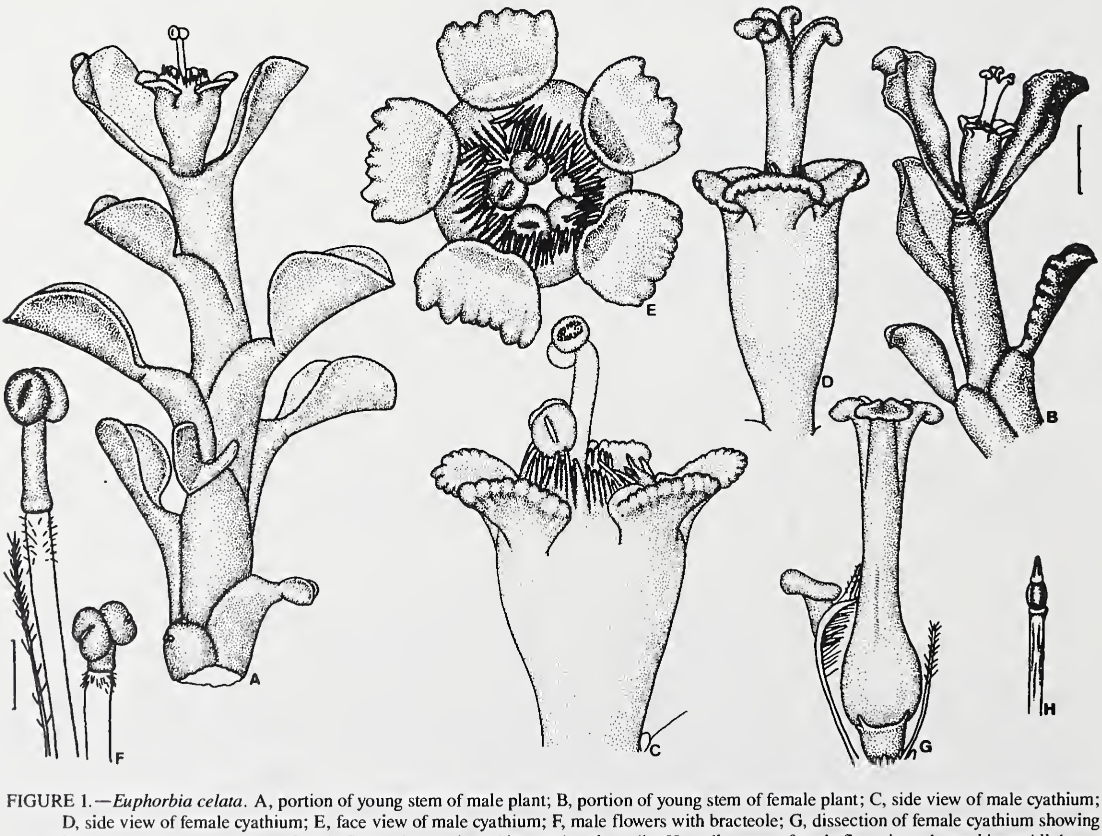

FIGURE 1.—*Euphorbia celata*. A, portion of young stem of male plant; B, portion of young stem of female plant; C, side view of male cyathium; D, side view of female cyathium; E, face view of male cyathium; F, male flowers with bracteole; G, dissection of female cyathium showing involucral gland, part of lobe, female flower, bracteole and bracteole primordia; H, rudimentary female floret in male cyathium. All drawn from *Bruyns 3704*, north of Vredendal. Scale bar: A, B, 3 mm; C–H, 1 mm.

on low hills south of Komaggas and in the numerous populations around Lekkersing, the stems are generally shorter and thicker with more densely arranged, more compressed tubercles. However, in these localities and in the hills just north of Komaggas (where plants were seen relatively sheltered among and inside bushes) any specimens that were even slightly protected showed new growth very similar to that from the southern portion of the distribution range.

North of Vredendal and along the Groen River the leaves of *E. celata* are usually 3–6 mm long. North of this they are often much smaller (as short as 1.5 mm) and their size is dependent on the situation of the plant (in sheltered branches they are still 3–4 mm long). The leaf is about as long as or longer than the tubercle to which it is affixed and in this respect is exactly as in *E. miscella*.

In *E. celata* (as in *E. miscella*) a terminal cyathium is produced, subtended by 2–3 leaf-like bracts in the axils of which further cyathia may develop. This is different to the situation in *E. namuskluftensis* where the cyathia are solitary and are borne near the apex of the branch in the axils of the tubercles. In *E. namuskluftensis* each cyathium is 'borne on a short, glabrous, bracteate peduncle' (Leach 1983: 190). This is lacking in both *E. celata* and *E. miscella*.

For *E. miscella* and *E. celata* the dimensions of the cyathia are summarized below (measurements based on Figure 1 for *E. celata* are given in brackets after Dyer's data; measurements based on *Bruyns 4637* are given in brackets after Leach's data for *E. miscella*.

E. miscella (Leach 1984a)
Male cyathium: up to 4.5 × 3.5 (4.0 × 2.5–3.0 mm), stipe 2–4 mm long (1–2 mm long), pedicels glabrous. Female cyathium: 3.5 × 4.5 (2.0–2.5 × 2.0 mm), style ± 2.5 mm long, capsule 7 mm diam.

E. celata (Dyer 1974)
Male cyathium: 4 × 4 mm (3.5 × 4.5 mm), peduncle 4 mm (1 mm) (pedicels sparsely pubescent towards apex). Female cyathium: 4.0 × 1.5 (3.0 × 2.5 mm), style 2.5 mm long (4 mm long, part protruding from involucre 2.5 mm long), capsule 5.5–6.0 mm diam.

The material on which Figure 1 is based was collected at the type locality of *E. celata* but differs from the flowering material seen by Dyer (1974). *Bruyns 4637* was collected from near the type locality of *E. miscella*. It is highly unlikely that more than one very similar species occurs at these localities and thus one is compelled to accept that variability occurs in *E. celata*, as is to be expected in most species. The small differences in the measurements between the material from north of Vredendal and that from Lekkersing are not considered to be significant and the remarkable similarity between Leach's *E. miscella* and *E. celata* forces one to the conclusion that these two represent the same species.

Specimens examined

CAPE.—2816 (Oranjemund): Kortdoringberg, (–DA), *Van Jaarsveld 5421A* (NBG). 2817 (Vioolsdrift): 10 km N of Lekkersing, (–CC), *Bruyns 4638* (BOL); Lekkersing, (–CC), *Marloth 12441* (STE). 2917 (Springbok): south of Lekkersing, (–AA), 18 July 1970, *Wisura 1622* (NBG); *Williamson 3323* (BOL), *3206* (NBG); *Leach 16545* (NBG); N of Gemsbokvlei, (–AA), *Bruyns 4637* (BOL); hills N of Komaggas, (–CD), *Bruyns 4617* (BOL); S of Komaggas, (–CD), *Bruyns 4595* (BOL). 3017 (Hondeklip Bay): Swartlintjies River, (–AB), *Bruyns 3556* (BOL); Groen River, (–DD), *Hall 4282* (NBG); *Bruyns 1733* (BOL). 3118 (Vanrhynsdorp): north of Hol R. Station, (–AD), *Hall 4722* (PRE); *Bruyns 3704* (BOL).

E. quadrata *Nel* in Jahrbuch der Deutschen Kakteengesellschaft: 42 (1935). Type: *Herre sub SUG 6519* (STE, holo.!; BOL, iso.!).

E. francescae Leach: 563 (1984b). Type: *Williamson 3248* (NBG!).

Euphorbia quadrata has been remarkably rarely collected. Originally discovered by Hans Herre in 1930 in the Stinkfontein Mountains, it was rediscovered by Oliver, Tölken & Venter in 1977 and since then only three collections seem to have been made. This is partly due to the remoteness of the areas in which it occurs and also to the inconspicuousness of the plants. On the summit of the Cornellsberg they grow fully exposed, forming small, densely branched, rounded shrubs with somewhat of an 'alpine shrublet' habit. However, lower down they were found to reach 1 m in height but were easily overlooked due to their nondescript appearance with large numbers of slender, scarcely succulent twigs and few leaves. At another locality further to the west they were common on the sheltered upper southwestern slope of a peak, growing inside other bushes and among rocks and were again inconspicuous despite being up to 0.5 m tall. It appeared that any branches projecting from the sheltering bushes were soon eaten back, and exposed plants were found grazed right back to the main stem.

In *E. quadrata* a complex system of thickened, brown, root tubers develops. The main stem may be up to 25 mm thick and this branches under the soil surface into more slender roots which are swollen at intervals into sausage-like tubers up to 30 mm thick. The aerial stems have a peculiar colouration: the youngest tissue usually to just below the leaves is a striking red-purple after which it is striped lengthwise through the splitting of this reddish bark. The reddish hue disappears after one season and older stems are covered with a uniformly greyish bark and have a somewhat rubbery consistency, not becoming truly woody (Figure 2).

As is usual in bisexual *Euphorbia* cyathia, the female flower appears first and the free parts of the styles are fully divergent after 3–5 days (Figure 2B, G). The female flower in *E. quadrata* remains erect for about 10 days and then bends downwards through the space left by the missing involucral gland just as the male flowers begin to appear (Figure 2C, D). If no pollination takes place, the style shrivels up within two days of its becoming fully recurved. If pollination does take place, the style gradually becomes erect and the ovary begins to swell. It has been found that an interval of several months may occur between pollination and the onset of development of the ovary. Colours observed in the flowers are unusual: the male pedicel is pale translucent green, the filament bright pinkish red and the anther is yellow lined with red along the pore; the female pedicel is greyish green except for red just beneath the ovary (the rudimentary calyx), the ovary is dark green and the styles are pink.

FIGURE 2.—*Euphorbia quadrata*. A, portion of young stem; B, G, side views of young cyathium with female floret still erect; C, side view of cyathium with female flower recurved; D, H, face views of cyathium; E, I, dissection of cyathium showing involucral lobe, male flowers, female flower and some bracteoles; F, cluster of male flowers. B–F drawn from *Bruyns 4044* (Cornellsberg summit); A, G, H, I from *Bruyns 3936* (Vandersterrberg). Scale bar: A–D, G, H, 3 mm; E, F, I, 1 mm.

Euphorbia quadrata and *E. francescae* both come from the summit of the Stinkfontein Mountains. *E. francescae* is given as differing from the former by 1, its much smaller plants with very short, tuberculate branches (± 30 mm long); 2, longer male flowers; 3, subglobose ovary; 4, very much shorter styles which are free almost to the base.

I have visited the summit of the Cornellsberg to investigate *Euphorbia francescae*. Compared to the type specimen, which is a remarkably minute plant, others at the same locality formed shrublets up to 200 mm tall and the same in diameter (as observed also by *Oliver et al.* on their specimen). All specimens seen were much stunted by grazing and by the heavy winds which sweep across this very exposed mountain top and this clearly explains the fact that they were much smaller than either the plants seen further down the mountain or the specimen cultivated at Stellenbosch by Herre (the type of *E. quadrata*). Their branches were therefore unusually short. Nevertheless, the 30 mm given by Leach for the length of the branches was observed to be on the small side and 30–100 mm would be more accurate. Leach considered Nel's species to be without small tubercles on the stems and Nel (1935) does not mention them in his description, but they are clearly present on the isotype specimen at BOL.

Nel does not mention the size of the male flowers. Leach (1984b: 567) gives the filaments in *E. francescae* as ± 1.5 mm long and states that they are longer than in *E. quadrata*. In Figure 2C the protruding male flower has a filament 2 mm long whereas in Figure 2E the filament is slightly less than 1.5 mm long. On the isotype of *E. quadrata* (BOL) the filaments are 2 mm long. Therefore I see no basis for Leach's statement about the relative sizes of the male flowers.

The styles of *E. quadrata* were given by Nel as 9 mm long. Leach gives them for *E. francescae* as '± 1.5 mm long, free almost to the base'. In Leach's illustrations (1984b: fig. 2.2) the styles are a little over 2 mm long with fused and free parts almost exactly equal in length. The somewhat thickened base that he shows (which he obviously did not include when measuring the style) has not been found in other material from the same site and is probably due to the styles already having begun to dry out (as pointed out above, this happens quickly after the female flower becomes recurved, if pollination has not occurred). In my collections the lengths of the styles were 3.5 mm on the Cornellsberg and 8 mm on the Vandersterrberg. These measurements are from very few specimens (one plant in the first case and three in the second) but even from these and including Nel's data, it is clear that *E. quadrata* varies considerably in this character so that this distinction is meaningless.

I conclude that it is not possible to distinguish *E. francescae* from *E. quadrata* with any certainty. The name *E. francescae* is therefore placed into synonymy.

Specimens examined

CAPE.—2816 (Oranjemund): Vandersterrberg, (—BD), *Bruyns 3936* (BOL). 2817 (Vioolsdrif): Cornellsberg, (—CA), *Oliver, Tölken & Venter 697* (PRE); *Williamson 3248* (NBG); *Bruyns 4044* (BOL); near summit of Stinkfontein Mountains, *Herre sub SUG 6519* (STE, holo.; BOL, iso.).

E. exilis *Leach* in Leach & Williamson, South African Journal of Botany 56: (1990). Type: *Leach & Bayer 17129* (NBG!).

E. glandularis Leach & Williamson: 75 (1990). Type: *Leach & Hilton-Taylor 17019* (NBG!).

Leach & Williamson (1990: 77) gave *E. exilis* (Figure 3) as occurring mainly on the Knersvlakte and *E. glandularis* in a small area to the northwest of Steinkopf (Leach & Williamson 1990: 76). More recently similar plants have been collected near Nigramoep (northwest of Springbok) and north of the Groen River (west of Garies). Since the plants are not readily distinguishable, except by an experienced collector, from the much commoner *E. ephedroides* E. Mey. ex Boiss. and members of the *E. decussata* complex, the species will probably be found in much of the intervening territory in due course.

Leach & Williamson distinguished *E. exilis* from *E. glandularis* by the 'smaller stature (300–400 mm as opposed to 0.6–1.0 m), its densely branched, clump-forming

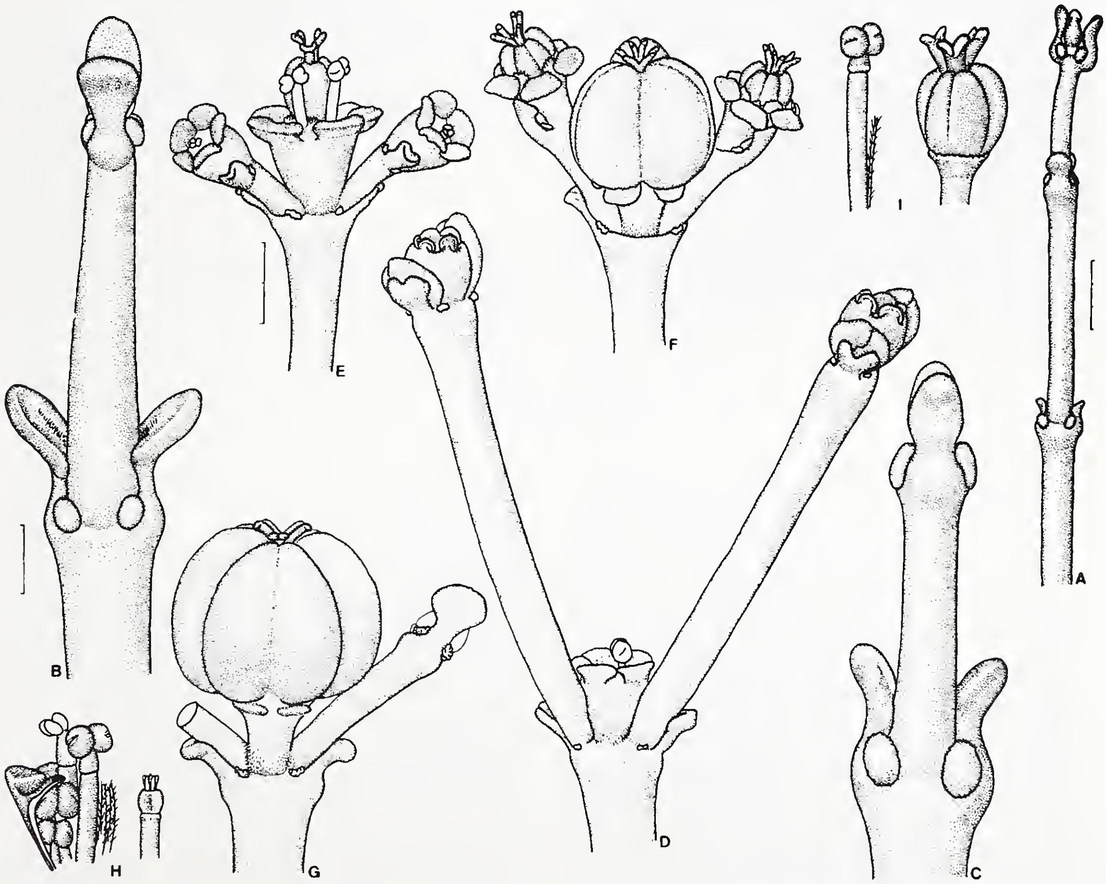

FIGURE 3.—*Euphorbia exilis*. A–C, portion of young stem; D, older male cyathium with two developing males on axillary branches; E, bisexual cyathia; F, female cyathia with one capsule nearing maturity; G, female cyathium with capsule near maturity; H, dissection of male cyathium showing involucral gland, part of lobe, male flowers and rudimentary female flower (separated); I, male and female flowers from separate (unisexual) cyathia. A, C, D, G drawn from *Bruyns 3214* (Nigramoep); B, H, from *Bruyns 3835* (Groen River); E, F, I from *Bruyns 3225* (N of Vredendal). Scale bar: A, 3 mm; B, C, H, I, 1 mm; D–G, 2 mm.

habit with soft, more slender branches, much smaller stipular glands, its frequently pink involucres and maroon bracts, its smaller capsule which is not ribbed in the sinuses and is borne on a longer pedicel, styles which are not appressed to the top of the capsule, and less prominently keeled seeds which are only ± 1.2 mm thick as opposed to 1.6 mm' in *E. glandularis*.

Plants collected near Nigramoep were 300–400 mm tall and thus, although geographically closest to *E. glandularis*, were actually more similar in stature to *E. exilis*. They were also extremely densely branched, as were those along the Groen River, far more so than plants seen at Hol River (Knersvlakte) but very similar to those seen at Quaggaskop on the Knersvlakte. Plants from the Groen River had slightly smaller stipular glands than those from Nigramoep (compare Figure 3B & 3C). Stipular glands of this size are also found on specimens from the Knersvlakte [*Hall 3734* (NBG) and others] and the minute stipular glands shown by Leach & Williamson (1990: fig. 4.9) had perhaps already dried out when drawn and were thus a fraction of their fresh size (Figure 3).

Recent collections suggest that the length of the female pedicel is an unreliable character. In particular, in *E. glandularis* the capsule is shown to squash the involucre on development (Leach & Williamson 1990: fig. 3.10) whereas in *E. exilis* this is not the case. In the material figured here from near Nigramoep (Figure 3G) the pedicel is slightly longer than that of a specimen from the Knersvlakte (Figure 3F). As can be seen in Figure 3E, F & I, the styles vary significantly in length at a single locality (Knersvlakte again), being quite close to the ovary (more like *E. glandularis*) in 3F & I and more erect in 3E (more like *E. exilis*). In the plant from Nigramoep (Figure 3G) they are much closer to the ovary, though not as closely adpressed as shown by Leach & Williamson for *E. glandularis*. The difference in the length of the united part of the styles (± 0.5 mm) and the 0.4 mm difference in thickness of the seeds given by Leach, are considered to be of questionable significance. Thus one of these names is unnecessary and *E. glandularis* is reduced to synonymy.

Specimens examined

CAPE.—2917 (Springbok): Klipfontein, (–BA), *Williamson 3773, 3789; Leach & Hilton-Taylor 17019* (all NBG); NE of Nigramoep, (–BC), *Bruyns 3214* (NBG). 3017 (Hondeklip Bay): 5 km NW Baievlei, (–DB), *Bruyns 4590* (BOL); 2 km towards Soutfontein, (–DB), *Bruyns 4588* (BOL); north of Groen River, (–DB), *Bruyns 3835* (BOL). 3018 (Kamiesberg): Kamagab, (–CD), *Bruyns 4586* (BOL). 3118 (Vanrhynsdorp): north of Vredendal, (–AD), *Hall 3734* (NBG); *Bruyns 3225* (NBG); Quaggaskop, (–BC), *Leach & Hilton-Tayor 16994* (NBG); *Bruyns 4035* (BOL); Hol River, (–CB), *Leach & Hall 14180* (NBG); Aties, (–DA), *Leach & Bayer 17129* (NBG).

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P. BRUYNS*

* Bolus Herbarium, University of Cape Town, Private Bag, Rondebosch 7700.
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FABACEAE

THE IDENTITY OF *ARGYROLOBIUM OBSOLETUM* AND THE CORRECT NAMES FOR SOME SPECIES OF *POLHILLIA* (CROTALARIEAE)

The genus *Polhillia* C.H. Stirton comprises seven rare and highly localised species, all of which are endemic to the southwestern Cape Province of South Africa. The generic circumscription of Stirton (1986a) was slightly broadened by Van Wyk & Schutte (1989) to include two species that were previously misplaced in *Argyrolobium* Eckl. & Zeyh. and *Melolobium* Eckl. & Zeyh. The species of *Polhillia* all have the bilabiate calyx of *Argyrolobium* and *Melolobium* and also have a similar combination of quinolizidine alkaloids (Van Wyk *et al.* 1988; Van Wyk & Verdoorn 1990), but can easily be distinguished from the two genera by the absence of true peduncles (Van Wyk & Schutte 1989). The internode directly below the inflorescence is elongated to function as a peduncle, a condition that can be recognised by the presence of a foliage leaf at the apex of the pseudo-peduncle. Other diagnostic characters are the woody habit, conduplicate leaflets, virtual absence of bracts and bracteoles, sheathing stipules, short calyx, pubescent corolla, imbricate keel petals and a chromosome number of 2n = 32 (Stirton 1986a; Van Wyk & Schutte 1989).

In considering various species for inclusion in the new genus, Stirton (1986a) overlooked *Argyrolobium obsoletum* Harv. Harvey (1862) queried the correct taxonomic position of this species by inserting a question mark behind the generic name. The holotype in the Thunberg collection in Uppsala clearly belongs to the type species of *Polhillia*, hitherto known as *P. waltersii* (C.H. Stirton) C.H. Stirton. A name change is therefore unavoidable. I am also using this opportunity to change the gender of some specific epithets that were not given in the correct form when species were transferred from *Argyrolobium* and *Melolobium* by Stirton (1986a) and Van Wyk & Schutte (1989). To avoid confusion, all known species of *Polhillia* are included in the following synonymy.

Polhillia *C.H. Stirton* in South African Journal of Botany 52: 167 (1986a); Van Wyk & Schutte: 397 (1989); Van Wyk: 265–288 (1991).

Lebeckia Thunb. subgenus *Plecolobium* C.H. Stirton: 318 (1981). Type: *Polhillia waltersii* (C.H. Stirton) C.H.

Stirton. [now *P. obsoleta* (Harv.) B-E. van Wyk, see below].

1. **P. brevicalyx** *(C.H. Stirton) Van Wyk & Schutte* in Kew Bulletin 43: 420 (1989).

Argyrolobium brevicalyx C.H. Stirton: 443 (1984). Type: *Burgers 3188* (K!, holo.; STE!, iso.).

2. **P. canescens** *C.H. Stirton* in South African Journal of Botany 52: 174 (1986a). Type: *Bayer 3104* (NBG!, holo.).

3. **P. connata** *(Harv.) C.H. Stirton* in South African Journal of Botany 52: 174 (1986a), as '*P. connatum*'. Type: *Thom 37* (K!, holo.).

4. **P. involucrata** *(Thunb.) Van Wyk & Schutte* in Kew Bulletin 43: 420 (1989), as '*P. involucratum*'.

Psoralea involucrata Thunb.: 607 (1823). *Argyrolobium involucratum* (Thunb.) Harv.: 75 (1862). *Melolobium involucratum* (Thunb.) C.H. Stirton: 355 (1986b), as '*M. involucratum* (Harv.) C.H. Stirton'. Type: *Thunberg s.n. sub UPS-THUNB 17575* (UPS!, lecto., chosen by Stirton 1986b).

5. **P. obsoleta** *(Harv.) B-E. van Wyk*, comb. nov.

Argyrolobium obsoletum Harv., Flora capensis 2: 70 (1862). Type: Cape, without precise locality, *Thunberg s.n. sub UPS-THUNB 16504* (UPS!, holo.).

Lebeckia waltersii C.H. Stirton: 318 (1981). *Polhillia waltersii* (C.H. Stirton) C.H. Stirton: 173 (1986a). Type: *Rourke 1484* (K!, holo.; NBG!, STE!, iso.).

Aspalathus sericea sensu Thunb.: 574 (1823) non DC.

P. obsoleta is known only from one locality at Worcester, where the first recent collection was made in 1977 (Stirton 1986a). A specimen not seen by Stirton (1986a) however, indicates that the species may have been much more widely distributed in an area that is now largely under wheat cultivation. This specimen, *Edwards s.n. sub BOL 13438* (BOL), was collected at Porterville (3318 BB Cape Town) and sent to the Bolus Herbarium in 1909.

6. **P. pallens** *C.H. Stirton* in South African Journal of Botany 52: 171 (1986). Type: *Burgers 2633* (STE!, holo.; K!, STE!, iso.).

7. **Polhillia** sp. A. [see Stirton: 178 (1986a)].

Stirton (1986a) expressed uncertainty about the identity of an anomalous specimen, *Hutchison 253* (K), which was previously included by Stirton (1981) under *L. waltersii (P. obsoleta)*.

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B-E. VAN WYK*

* Department of Botany, Rand Afrikaans University, P.O. Box 524, Johannesburg 2000.
MS. received: 1991-06-11.

PROTEACEAE

THE CORRECT AUTHOR CITATION FOR *PARANOMUS REFLEXUS*

In the most recent revision of *Paranomus* (Levyns 1970), the authority for *Paranomus reflexus* is given as *P. reflexus* (Phill. & Hutch.) N.E. Br. in *Transactions of the Royal Society of South Africa* 21: 263 (1933). This citation is also used in Gibbs Russell *et al.* (1987). However, an earlier combination made by Fourcade in 1932 has been overlooked. Curiously, Fourcade's combination was published in the same volume of the same journal as N.E. Brown's was, namely *Transactions of the Royal Society of South Africa* vol. 21, but in part 1 published in December 1932, whereas N.E. Brown's combination appeared in part 3 published in November 1933.

The correct author citation for this species is therefore *Paranomus reflexus* (Phill. & Hutch.) Fourcade in *Transactions of the Royal Society of South Africa* 21: 97 (1932).

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J.P. ROURKE*

* National Botanical Institute, Kirstenbosch, Private Bag X7, Claremont 7735.
MS. received: 1991-10-29.

GOMPHILLACEAE (LICHENES)

A NEW SPECIES OF *BULLATINA* FROM THE TRANSKEI WILD COAST

Bullatina viridis *Brusse*, sp. nov.

Thallus crustosus, foliicola, viridis, usque ad 7 mm diam., laevis, trichomatibus hyphophorisque instructus; prothallus argenteo-albidus. *Trichomata* (Figurae 4 & 5) albida, simplicia, arcuata, usque ad 1.2 mm longa, basi circa 50 μm crassa, ad apicem acuta. *Hyphophora* (Figurae 4 & 5) piliformia, albida, erecta, 0.22–0.30 mm alta, basi 20–30 μm crassa, ad apicem obtusa; ex apicibus fasciculus lacrimiformis conidiophororum et catenarum conidiorum cellulis algarum pendens. *Conidiophora* (Figura 6) hyalina, leviter ramosa, septata. *Cellulae conidiogenae* nonnihil inflatae, terminales. *Conidia* concatenata (Figura 6), holoblastica, acropeta, hyalina, simplicia, ellipsoidea vel clavata, 6.0–8.5 × 1.3–2.0 μm. *Cortex* (superior) monostratus, 3–5 μm crassus, paraplectenchymatus, cellulis 3–5 μm diam. *Stratum gonidiale* 15–20 μm crassum. *Algae* coccoideae, virides, 4.5–11.0 μm diam. *Apothecia* viridia, sessilia, usque ad 0.4 mm diam. (Figura 4). *Excipulum thallinum* 25–30 μm crassum, cellulas algarum continens, crystallis destitutum. *Excipulum proprium* reductum, hyalinum, prosoplectenchymatum, 10–15 μm crassum. *Hypothecium* destitutum. *Hymenium* hyalinum, J–, 55–80 μm altum. Paraphyses leviter ramosae anastomosaeque vel fere simplices, parallelae, septatae, ecapitatae, bene gelatinosae, luminibus circa 0.8 μm crassis. Epihymenium 5–8 μm crassum, cum gonocystibus, 2.5–5.0 μm diam., crystallis destitutum. *Asci* late clavati, parietibus J– hyalinis, apici leviter incrassatis, ascoplasmate J vinoso-rubescente. *Ascosporae* singulae, 30–60 × 10–22 μm, hyalinae, muriformes, 11–18 × 2–5-loculares, halonatae, ovales, extremis obtusis, J–, parietibus tenuibus, cyanophilis, interdum in pycnidia mutantes, vel in spermatia, hyalina, 3–4 × 0.7 μm, fatiscentes. *Pycnidia propria* non visa.

FIGURE 5.—*Bullatina viridis* Brusse, camera lucida drawing of a trichome and hyphophores, showing the teardrop-shaped conidial mass. *F. Brusse 5864*, holotype. Bar = 0.1 mm.

FIGURE 4.—*Bullatina viridis* Brusse, habit. *F. Brusse 5864*, holotype. Scale in mm.

TYPUS.—Transkei, 3228 (Butterworth): Dwesa Nature Reserve. About 1 km from campsite on road to mPume gate. On living fronds of the cycad *Encephalartos villosus* Lem., in understorey vegetation of coastal forest. Alt. 40 m (–BD). *F. Brusse 5864*, 1991-01-05 (PRE, holo.; BM, iso.). Figurae 4, 5 & 6.

Thallus crustose, foliicolous, green, up to 7 mm across, smooth, with trichomes and hyphophores; prothallus whitish with a silvery sheen. *Trichomes* (Figures 4 & 5) completely whitish, simple, arcuate, up to 1.2 mm long, about 50 μm thick at base, apex acute. *Hyphophores* (Figures 4 & 5) piliform, whitish, erect, 0.22–0.30 mm tall, 20–30 μm thick at base, apex obtuse, a teardrop-shaped bundle (when wet) of conidiophores and chains of conidia hang down from apex, which contains algal cells in its core. *Conidiophores* (Figure 6) pendant, hyaline, sparsely branched, septate. *Conidiogenous cells* somewhat swollen, terminal. *Conidia* concatenate (Figure 6), holoblastic, acropetal, hyaline, simple, ellipsoid to clavate, 6.0–8.5 × 1.3–2.0 μm. *Upper cortex* single-layered, 3–5 μm thick, paraplectenchymatous, cells 3–5 μm diam. *Algal layer* 15–20 μm thick. *Algae* coccoid, green, 4.5–11.0 μm diam. *Apothecia* green, sessile, up to 0.4 mm diam. (Figure 4). *Thalline exciple* 25–30 μm thick, containing algal cells, crystals (of calcium oxalate) absent. *Proper exciple* reduced, hyaline, prosoplectenchymatous, 10–15 μm thick. *Hypothecium* absent. *Hymenium* hyaline, J–, 55–80 μm high. Paraphyses lightly branched and anastomosed to nearly simple, parallel, septate, ecapitate, strongly gelatinized, lumens about 0.8 μm thick. Epihymenium 5–8 μm thick, with gonocysts, 2.5–5.0 μm diam., crystals (of calcium oxalate) absent. *Asci* broadly clavate, 1-spored, wall J– hyaline, somewhat thickened towards apex, ascoplasma J wine-red. *Ascospores* 30–60 × 10–22 μm, hyaline, muriform, 11–18-locular × 2–5-locellate, halonate, oval, ends obtuse, J–, walls thin, cyanophilic (the walls stain deep blue in lactophenol Cotton Blue), sometimes changing into pycnidia, or disintegrating into hyaline spermatia, 3–4 × 0.7 μm. *Proper pycnidia* not seen.

This new species is a very distinct species from a macroscopic habit point of view. The whole lichen is green in colour, and the proper exciple does not crack away from the thalline exciple except very rarely in old specimens. The colour may be due to the fact that the whole lichen lacks calcium oxalate crystals, which are common in the greyer species.

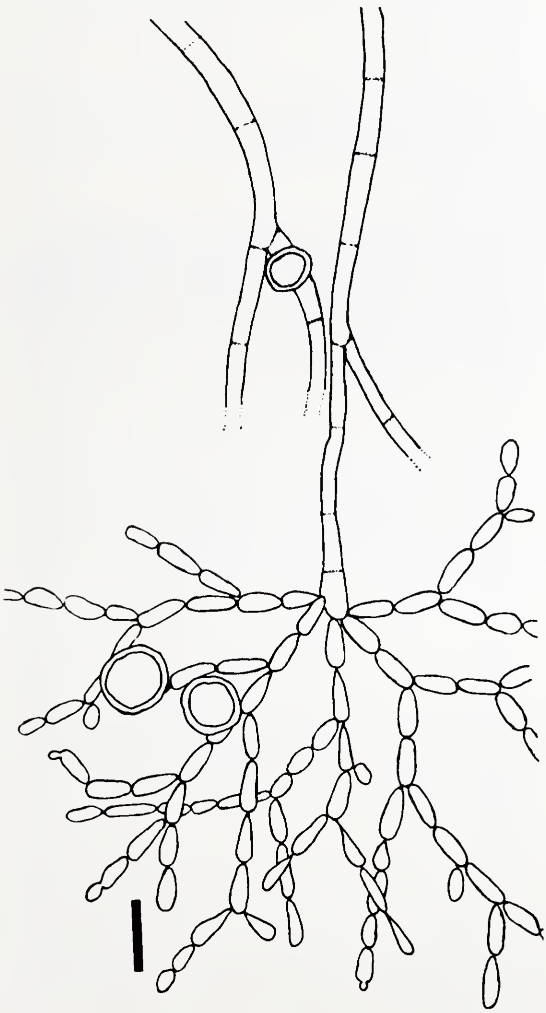

FIGURE 6.—*Bullatina viridis* Brusse, camera lucida drawing of the conidiophores and chains of conidia. *F. Brusse 5864*, holotype. Bar = 10 μm.

The thallus bears whitish trichomes and much smaller whitish hyphophores, quite abundantly. The hyphophores, which represent the anamorph of this lichen, are of the hanging teardrop type, which is also found in *Bullatina aspidota* (Vain.) Vězda & Poelt, until now the only species of *Bullatina* (Vězda 1979: fig. 9; Vězda & Poelt 1987). However, the hyphophores and trichomes are similar in size in *B. aspidota* (0.5–0.6 mm long), whereas in *B. viridis* they are clearly dimorphic—the hyphophores only reaching 0.3 mm high and being stubble-like, whereas the trichomes are much longer, becoming 1.2 mm long in some cases.

The genus *Gyalectidium* Müll. Arg., closely related to the genus *Bullatina* Vězda & Poelt, produces a completely different anamorph in the form of a small erect scale, which may be variously ciliate or ragged along the upper edge, with the conidial mass in the axil of this scale (Serusiaux & De Sloover 1986; Vězda 1979, 1983).

This new species is not likely to be confused with the only other *Bullatina* species, *B. aspidota* due to the latter's relatively thick thallus which is white due to calcium oxalate crystal encrustation. The apothecia are deeply sunken into the thallus as well (Santesson 1952: fig. 64) and the ascospores are larger (42–80 × 20–32 μm) than those of *B. viridis* (30–60 × 10–22 μm).

Superficially *B. viridis* may be mistaken for a *Tricharia* with white trichomes, especially one with epithecial gonocysts present, such as in *T. vulgaris* (Müll. Arg.) R. Sant. *T. vulgaris* has, in fact, got ascospores of a very similar size range to *B. viridis*, but *T. vulgaris* lacks trichomes and possesses a stalked-auriculoid hyphophore (Kalb & Vězda 1988; fig. 2), rather than the teardrop hyphophore of *B. viridis*, and many other *Tricharia* species (Kalb & Vězda 1988; Vězda 1979). *T. vulgaris*, like all other *Tricharia* species, has a well-developed proper exciple which is paraplectenchymatous and 20–30 μm thick under the hymenium, and thicker on the flanks. This degree of exciple development is lacking in *B. viridis*. On the other hand, the apothecia of *Tricharia* lack a thalline exciple and stand clear of any thalline tissue, whereas those of *Bullatina* possess a thalline exciple, usually referred to as being immersed in the thallus (cryptolecanorine). However, whatever the situation is, the flanks of the hymenium have tissue containing algae in *B. viridis*, which is not the case in all *Tricharia* species, including *T. vulgaris*.

Thus far, this new species has only been collected at the type locality, Dwesa Forest on the Transkei Wild Coast, but will undoubtedly be found at other forested localities in warm subtropical and tropical areas.

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F. BRUSSE*.

* National Botanical Institute, Private Bag X101, Pretoria 0001.

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MORACEAE

NEW RECORDS OF *FICUS* SPECIES AND THEIR POLLINATORS ON GRAND COMORE

The Comoros consist of four major islands of volcanic origin, the largest and geologically youngest of which is Grand Comore (Ngazidja). The fig trees (*Ficus* spp., Moraceae) of the Islands were revised by Berg (1986), who recognised nine *Ficus* species, five of which were recorded from Grand Comore. The nine Comoran *Ficus* species include two species that are also present on the African mainland and six species shared with Madagascar. There is also one endemic species, and one of the species shared with Madagascar is represented by an endemic subspecies.

Fig trees are pollinated exclusively by fig wasps (Hymenoptera: Agaonidae). Knowledge of the fig wasps of the Comoro Islands is minimal, with just a single record from Mayotte of *Allotriozoon heterandromorphum*, the pollinator of *F. lutea* (Wiebes 1974). This report describes the results of a survey of *Ficus* species and their pollinators carried out on Grand Comore in July 1990. Specimens of eight *Ficus* spp. were collected, of which four were new to the island. The pollinators of four of these *Ficus* species were also collected. These included the pollinator of one of the taxa endemic to the islands, which had not been recorded previously. Plant collection codes (CH) and the herbarium where the material is deposited are indicated. The wasps are retained by the author.

F. pachyclada Bak. subsp. *pachyclada*

North of Magoudjou, near South African Research Farm, *CH1* (RUH), 10 m, free-standing among rocks in remnant woodland, 25-vii-90. Previously recorded from Madagascar. Additional uncertain records, based on juvenile specimens, from Grand Comore. Previous records cited in Berg (1986).

F. bojeri Bak.

Near Dzamadjou, 6 km north of Moroni, *CH2* (RUH), 4 m, free-standing tree along roadside, 22-vii-90; near Maoueni, *CH3* (RUH), 9 m, strangler along roadside, figs in leaf axils and projecting from the main trunk, 24-vii-90; near Maoueni, *CH4* (RUH), 13 m, large buttressed tree along roadside, 24-vii-90. Previously recorded from Madagascar, Seychelles and other islands in the Comoros. Previous records cited by Berg (1986). New records for Grand Comore.

F. sycomorus L.

Hadjambou, in the northeast of the island, *CH5* (RUH), 6 m buttressed tree in pasture, 23-vii-90. Pollinating wasp *Ceratosolen arabicus* Mayr, as in mainland Africa. The non-pollinating agaonid *Ceratosolen galili* also present. Widespread in Africa, Madagascar and other islands in the Comoros. Previous records cited in Berg (1986). New record for Grand Comore.

F. tiliifolia Bak.

Mount Karthala, above Moroni, *CH6* (RUH), at side of contour path in disturbed forest, one of a group of six 3–4 m saplings, 26-vii-90. Previously recorded from Madagascar and other islands in the Comoros. Previous records cited by Berg (1986). New record for Grand Comore.

F. lutea Vahl

Maoueni, 5 km north of Moroni, *CH7* (RUH), small strangler in remnant woodland, 22-vii-90; Maoneni-Grill forest, *CH8* (RUH), large free-standing tree in cleared pasture near forest, 24-vii-90. Pollinating wasp *Allotriozoon heterandromorphum* Grandi, as in mainland Africa. Widespread in Africa, Madagascar and other Indian Ocean islands. Previous records cited by Berg (1986).

F. rubra Vahl

Maoueni, 5 km north of Moroni, *CH9* (RUH), small strangler, 22-vii-90; Maoneni-Grill forest, *CH10* (RUH), small strangler, figs on pedicels in leaf axils and more or less sessile from major branches, 24-vii-90. Pollinating wasp *Nigeriella avicola* Wiebes, as on Aldabra (Wiebes 1975); southeast coast near Chamou Beach, *CH11* (RUH), large strangler on baobab, 27-vii-90. Recorded from Madagascar, the Comoros and other Indian Ocean Islands. Previous records cited by Berg (1986).

F. antandronarum (H. Perrier) C.C. Berg subsp. *bernardii* C.C. Berg

Maoneni-Grill forest, *CH12* (RUH), small strangler, mature figs yellow. Pollinating wasp *Elisabethiella* sp. indesc., 24-vii-90; Maoneni-Grill forest, *CH13* (RUH), small strangler, 24-vii-90. This subspecies is restricted to the Comoro Islands. Previous records cited by Berg (1986). New pollinator record for the subspecies and species (Wiebes & Compton 1990).

F. reflexa Thunb. subsp. *aldabrensis* (Bak.) C.C. Berg

Road between Moroni and Mt Karthala, *CH14* (RUH), scrub/plantation, at roadside, small strangler of Jack fruit, 26-vii-90; South Coast road, near Sima Ambonii, *CH15* (RUH), roadside, small strangler on baobab, 25-vii-90. This subspecies previously recorded from Aldabra and other islands in the Comoros. Previous records cited by Berg (1986). New record for Grand Comore.

Eight of the nine *Ficus* species known from the Comoro Islands were collected. The remaining species, *F. kartha-*

lensis C.C. Berg, was originally described from Grand Comore. Consequently, all the fig species known from the Comoros have now been recorded from Grand Comore.

The natural vegetation of Grand Comore consists of coastal and upland forest zones and a small area of heathland at the summit of Mt Karthala (Bijnens *et al.* 1987). In the lowlands, most of the original forest cover on the island has been converted to agriculture. The extent of native tree removal at lower altitudes is nonetheless variable, and *F. sycomorus* is not uncommon, either in remnant patches of disturbed forest or growing in pastures. The smaller strangler figs also persist at lower altitudes, if suitable host trees remain. At higher altitudes, forest cover is extensive on the active volcano Mt Karthala and there is a remnant Maoeni-Grill forest. *F. tiliifolia* and *F. antandronarum* subsp. *bernardii* were detected only in these areas.

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S.G. COMPTON*

* Department of Zoology and Entomology, Rhodes University, Grahamstown 6140.

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FABACEAE

A NEW SPECIES OF *PRIESTLEYA* FROM THE SOUTHWESTERN CAPE

Priestleya boucheri *Oliver & Fellingham*, sp. nov., in genere singularis propter florescentias occultas foliis subinvolucratis, bracteas aurantiacas, flores grandes, calycem subinaequalem, vexillum elongatum reflexum.

TYPE.—Cape, 3418 (Simonstown): Grabouw area, Kogelberg Reserve, Five Beacon Ridge, summit of ridge, 1 160 m, 20 May 1989, *Boucher & Oliver 5531* (STE, holo.; BOL, K, MO, PRE, S, iso.).

A low compact woody single-stemmed shrub up to 500 mm tall. *Stem* and *branches* leafy only in the ultimate 80–100 mm, the younger long villous, the older glabrous with prominent leaf scars, distinctly 3-ridged below the leaf scars with the main ridge below the leaf scar and the two smaller lateral ridges below the stipules, the bark yellowish brown and corky. *Leaves* spirally arranged, imbricate, erect, incurved, subsessile, 26–50 × 12–17 mm, linear-elliptic to narrowly obovate, acute rarely subobtuse, green but slightly glaucous, the younger silky villous all over, noticeably shaggy-edged with the hairs all pointing to the apex and longer on the adaxial surface, soon becoming almost glabrous with some adpressed old dark-brown hairs, margins yellow, veins yellowish, mucro minute and reddish brown, venation pinnate, stomata numerous and visible on both surfaces; stipules 2, minute, enlarging alongside the leaf scars.

Inflorescences 2-flowered fascicles on lateral absolute brachyblasts 1.0–1.5 mm long, mostly aggregated into 4- or 6-flowered synflorescences enclosed within the upper leaves at the ends of the main branches, flowers erect and arranged in a circle; pedicel 3 mm long, pubescent; bract 7.0–8.0 × 6.5 mm, very broadly ovate, shortly acuminate, at first creamy-green soon turning papery and yellow-brown, long ciliate, abaxially sparsely villous, adaxially villous, clasping the base of the calyx and the pedicel. *Calyx*: tube 7.5–10.0 × 5.0 mm, pale creamy-green, becoming papery and yellow-brown; lobes 5.0–5.5 mm long, the lowest subequal to or 0.5 mm longer than the others, the upper two lobes fused more than the others, free distally for 1 mm, darker in colour than the tube, villous, long ciliate. *Petals*: standard 25 × 6 mm, ovate-elliptic, reflexed over the fused calyx lobes in the mature flower, claw 4 × 2 mm with 2 basal lateral lobes 3 mm long, separated abaxially by 2 ridges and a median channel; alae 24 × 4 mm, oblong, falcate, obtuse, claw 3.5 mm long, lobe with an internal thickening in the upper part; keel 25.0 × 4.5 mm, navicular, acute, claw 2 mm long, lobes connate above for $^{2}/_{3}$ and below for $^{1}/_{2}$ their length. *Stamens* diadelphous, vexillary filament free, 26 mm long, the others connate for about 12 mm into a tube thickened at the base and with 2 knobs adjoining the free filament, the longest connate filament 28 mm and the shortest 21 mm long; anthers ± 1 mm long. *Ovary* ± 6 mm long, obliquely narrowly ovate, long, silky, villous, with forward pointing hairs; style 21 mm long, glabrous; *stigma* simple. *Fruit* 25 × 9 × 5 mm, including the remnant style base, 6-seeded, villous with appressed hairs pointing towards the apex, golden brown; seeds 4.5 × 2.0 mm, compressed, olive-brown with a white aril. Figure 7.

Diagnostic characters: *P. boucheri* is very distinct in the genus on account of the hidden inflorescences, the large flowers, the longer lower calyx lobe, the calyx being yellow-brown at maturity and the large but narrow standard which is reflexed over the calyx at maturity.

Discussion: this species was brought to our attention by C. Boucher who has made a special study of the

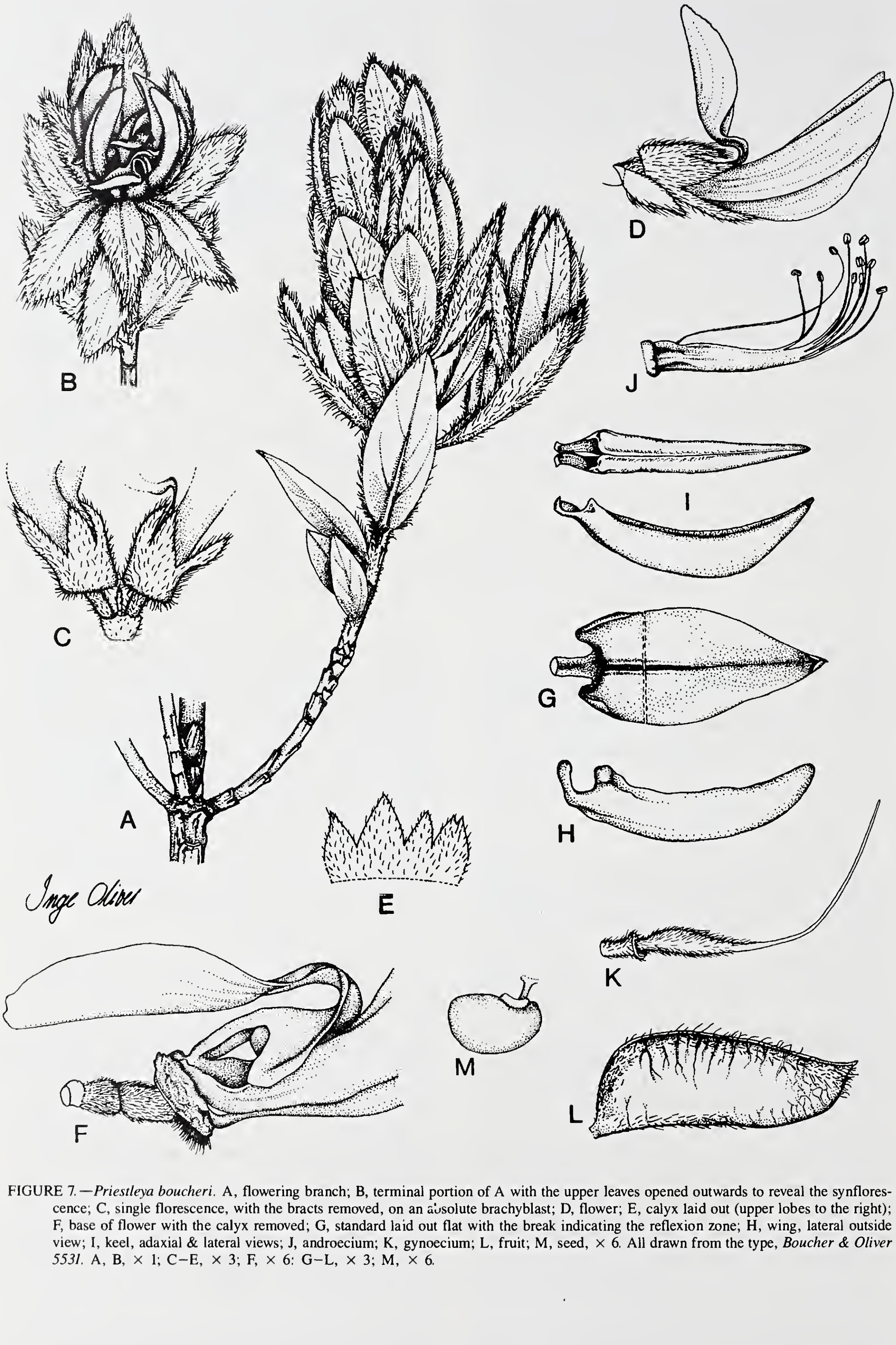

FIGURE 7.—*Priestleya boucheri*. A, flowering branch; B, terminal portion of A with the upper leaves opened outwards to reveal the synflorescence; C, single florescence, with the bracts removed, on an absolute brachyblast; D, flower; E, calyx laid out (upper lobes to the right); F, base of flower with the calyx removed; G, standard laid out flat with the break indicating the reflexion zone; H, wing, lateral outside view; I, keel, adaxial & lateral views; J, androecium; K, gynoecium; L, fruit; M, seed, × 6. All drawn from the type, *Boucher & Oliver 5531*. A, B, × 1; C–E, × 3; F, × 6: G–L, × 3; M, × 6.

vegetation and flora of the Kogelberg Reserve (Boucher 1977) and is currently involved with sensitive conservation matters in the area. His collection, made late in the year, was in fruit and remained unidentifiable, but tentatively placed near the genus *Liparia*. Subsequently further material, which was in a young flowering stage, was collected by D. le Maî tre in April during a survey of rare species in the Kogelberg area for the Department of Forestry. This enabled us to ascertain that the collections represented a remarkable new species quite unlike either of the two species of *Liparia* (Bos 1967). Material with fully open flowers was then obtained in late May to analyse in detail.

Knowing that the material was collected in the Kogelberg area, which had been visited many times by that veteran plant collector Thomas Stokoe during the period 1920 to 1955, a search was made for a collection of his in BOL and NBG including SAM. Two fruiting twigs came to light under the incertae of *Priestleya* in SAM, one collected in 1944 from just 'Kogelberg', the other in 1953 recorded from Five Beacon Ridge. While reading through the letters of Stokoe to the late W. & M. Cloete of Kleinmond [in the possession of EGHO], a reference was found, dated 1953, to an unknown *Priestleya* which he had not been able to collect in flower despite several attempts to do so. He mentioned it as growing on the crest of the Five Beacon Ridge near Kogelberg and a sketch of the locality was given. From this sketch it is clear that our type collection and Stokoe's note refer exactly to the same population.

Two distinct populations of this species are known to exist at present (Figure 8), separated by only 0.5 km. The type population on Five Beacon Ridge contained eight plants, two of which were seedlings. The population on the ridge towards Kogelberg (*Le Maî tre 401; Oliver 9139*) contained 10 plants, two of which were seedlings. In a detailed note accompanying his collection, Le Maî tre notes that the fire history showed that the area had been burnt in March 1976 and therefore the plants were probably 13 years old in 1989. He further records that R.A. Haynes and F.J. Kruger, also of the Department of Forestry, found another population of 10 plants to the southwest in 1981, but that only one dead plant could be located in 1986 due to a fire a few years earlier. All the populations were destroyed in a lightning-induced fire in February 1990 and will therefore have to regenerate from seed.

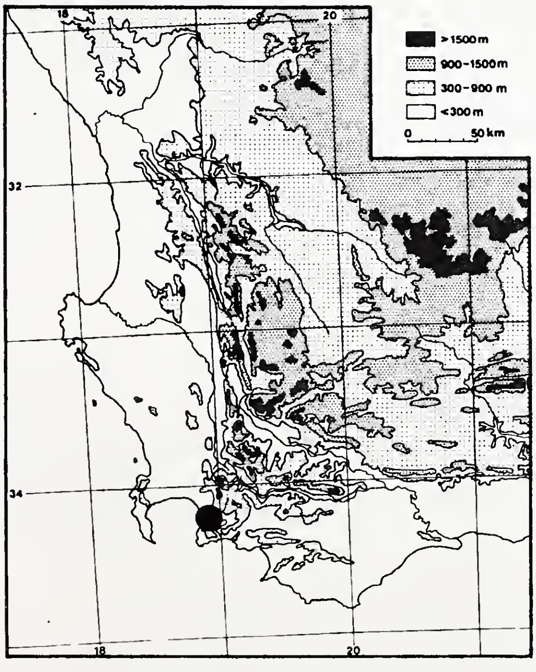

FIGURE 8.—Known distribution of *Priestleya boucheri*.

The large, flat, hairy leaves give the plants a remarkably proteoid facies similar to *Protea stokoei, P. caespitosa* and *Leucadendron gandogeri* which all grow in the immediate vicinity. The flowers are hidden from view from a distance and are only seen when the shrub is viewed from above, very much like the condition occurring in many species of *Leucadendron*. This is due to the large subterminal leaves which curve over the synflorescences. The bud and fruit stages are completely hidden. In the bud stage the flowers are erect with the standard covering the alae and the keel. In the mature flower the position of the standard becomes horizontal, i.e. perpendicular to the rest of the flower. This position is reached after a 180° bend occurring closely over the fused calyx lobes followed by a second, distally from and close to the first but 90° in the opposite direction (Figure 1D). With the standards of all flowers in the synflorescence assuming this position, the 'involucral' leaves are pushed open to expose the flowers in a cuplike formation (Figure 1B). After pollination, the second bend in the standard is straightened again, allowing the standard to be totally reflexed over the calyx lobes (Figure 1F). The involucral leaves then close over the synflorescence and hide the developing fruits completely.

The pollinating agent was not noted during the visit to the flowering population. However, the large size and whole arrangement of the flowers noted above strongly suggests visitation by a large bee.

The floral characters place the species very close to *Liparia* and in particular to *L. parva*. That genus is characterized by large narrow flowers each in the axil of a large petaloid bract, with the calyx very unequal, the lowest lobe being subpetaloid and much longer than the others. In the new species the calyx lobe is subequal to 0.5 mm longer than the other lobes. In *L. splendens*, however, the keel petals are held together by a most remarkable interlocking 'catch' system of the alae. The flower colour and structure is very similar to the lemon-yellow-flowered *L. parva* which is endemic in the southern Cape Peninsula, whereas the more widespread *L. splendens* has bright orange to reddish orange flowers. In *Priestleya* and *Xiphotheca* the flowers are generally smaller and have a very broad rounded standard and usually equal calyx lobes.

In the plant architecture and structure of the inflorescence this species is quite unlike *Liparia* and is identical to the genus *Priestleya sens. str.* (= *Priestleya* section *Priestleya*). In *Liparia* the flowers are borne in the axils of leaf-like bracts at the ends of main or leafy lateral branches, forming a simple condensed racemose florescence. This florescence, which in most cases is fairly heavy due to the number of large flowers, hangs downwards in a nodding fashion. It is also non-innovating and so further growth of the axis has to be initiated from an axillary bud on the upper side of the curved branch just below the florescence.

In the new species the flowers are borne in pairs at the ends of lateral absolute brachyblasts, i.e. extremely shortened and leafless branchlets. These 2-flowered florescences are grouped mostly in pairs or threes at the ends of the main branches to form a synflorescence which is enclosed within the involucre-like upper leaves (Figure 9). The florescences are non-innovating, but this does not affect the growth pattern of the plant as growth continues from the apical bud of the main axis in the centre of the synflorescence. On old branches the remains of some brachyblasts lower down clearly indicate the position of the synflorescences of previous years.

A detailed study of inflorescences in *Priestleya* and related genera has shown that three basic types can be distinguished (Schutte & Van Wyk in prep.): 1, simple terminal or subterminal racemes with a rachis extension, i.e. a sterile apical portion. This type can be many-flowered (*Liparia*) or few-flowered (*Priestleya hirsuta* and related species); 2, axillary 2- or 4-flowered fascicles, also with a sterile apical portion. The flowers are arranged in opposite pairs (decussate). This inflorescence type occurs in *Priestleya calycina* and related species and also *P. boucheri* (see Figure 7C where the small terminal sterile part can be distinguished); 3, axillary 2-flowered fascicles without a sterile apical portion, i.e. a simple determinate reduced inflorescence. This type is superficially similar to the previous type, but can easily be distinguished by the absence of a terminal sterile part. Section *Anisothea* of *Priestleya* has this type of inflorescence and, together with the non-intrusive base of the calyx and characteristic combination of alkaloids, these provide convincing supportive evidence for excluding the section from *Priestleya*. This was done by Ecklon & Zeyher (1836) who proposed the new generic name *Xiphotheca*.

Several species of *Priestleya* occur in the area around Kogelberg Peak and they are very striking plants. The two tall, almost tree-like species, *P. calycina* and *P. tomentosa* (*X. villosa*) have silvery leaves and conspicuous heads of bright yellow flowers. An as-yet-undescribed species occurs on the southern slopes of Five Beacon Ridge in Spinnekopsneskloof and was also collected by Boucher (*Boucher 1812*).

Chemical analyses of samples from both populations on the Kogelberg clearly indicate that this species contains alkaloids characteristic of *Priestleya sens. str.* and *Liparia parva* and none of the unique compounds found in *Xiphotheca* (Van Wyk *et al.* 1991). The new species has large amounts of quinolizidine alkaloids such as sparteine, 11,12-dehydrosparteine, lupanine, isolupanine and 13-hydroxylupanine. The relative quantities of these alkaloids are closely similar to the combinations found in other species of *Priestleya* (virtually identical to that found in *P. latifolia*, for example). *Liparia splendens* differs from *L. parva* in the much higher proportion of ammodendrine, but otherwise the alkaloids of *Liparia* are similar to those found in *Priestleya*. In contrast, *Priestleya* section *Anisothea* (= *Xiphotheca*) has a unique combination of alkaloids not found in *Priestleya sens. str.*, i.e. anabasine

FIGURE 9.—Diagram of the structure of a synflorescence in *Priestleya boucheri* consisting of three two-flowered florescences on lateral, non-innovating brachyblasts—dotted lines represent extended axes.

(a bipiperidyl alkaloid) and lupinine (a bicyclic quinolizidine).

The position of this new species is thus anomalous on account of its liparioid flowers and it shows the connection between the two genera. Indeed, the status of *Liparia* as a genus distinct from *Priestleya sens. str.* can be seriously questioned. Generic delimitation in the tribe Liparieae is currently under critical revision (Schutte & Van Wyk in prep.) because the present system does not reflect major discontinuities in intergeneric relationships.

Specimens examined

CAPE.—3418 (Simonstown): Kogelberg Reserve, Five Beacon Ridge, 1 160 m, 8-10-1980, mature fruiting, (−BB), *Boucher 4975* (STE); ibid., 20-5-1989, flowering, *Boucher & Oliver 5531* (BOL, K, MO, PRE, S, STE); ridge between Kogelberg and Five Beacon Ridge, 1 120 m, 22-4-1986, in bud, (−BB), *Le Maître 401* (PRE, STE); ibid., 1 130 m, 25-5-1989, flowering, *Oliver 9139* (PRE, STE): Kogelberg, 11-1944, mature fruiting, (−BB), *Stokoe in SAM 56330* (SAM); Five Beacon Ridge near Kogelberg, 9-1953, young fruit, (−BB), *Stokoe in SAM 65718* (SAM).

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E.G.H. OLIVER*, A.C. FELLINGHAM* and B.-E. VAN WYK**

* Stellenbosch Herbarium, National Botanical Institute, P.O. Box 471, Stellenbosch 7601.

** Department of Botany, Rand Afrikaans University, P.O. Box 524, Johannesburg 2000.

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The occurrence in southern Africa of the hepatic, *Symphyogyna brasiliensis* (Pallaviciniaceae)

S.M. PEROLD*

Keywords: hepatic, Metzgeriales, Pallaviciniaceae, southern Africa, *Symphyogyna brasiliensis*, *S. lehmanniana*

ABSTRACT

In Magill & Schelpe (1979) *Symphyogyna lehmanniana* is confirmed as occurring in southern Africa. Subsequently, however, Grolle (1980) reported that this name, which has been applied to a liverwort widespread in Africa, is a synonym of *S. brasiliensis*. To draw attention to this synonymy, a description of *S. brasiliensis*, illustrated with photographs, is given here, as well as an account of its distinguishing features and its distribution.

UITTREKSEL

In Magill & Schelpe (1979) word die teenwoordigheid van *Symphyogyna lehmanniana* in suidelike Afrika bevestig. Daarna berig Grolle (1980) egter dat hierdie naam, wat vir 'n wydverspreide lewermos in Afrika gebruik is, 'n sinoniem is van *S. brasiliensis*. Om die aandag op hierdie sinonimie te vestig, word 'n beskrywing van *S. brasiliensis*, geïllustreer met foto's, sowel as inligting oor sy onderskeidende kenmerke en verspreiding hier gegee.

INTRODUCTION

In Magill and Schelpe's (1979) checklist, *Symphyogyna lehmanniana* is listed as one of the species of *Symphyogyna* occurring in southern Africa.

Subsequently, however, Grolle (1980) concluded that this name, applied to a liverwort reported to be widespread in Africa, is a synonym of *S. brasiliensis*. During the course of his investigations Grolle had compared specimens assigned to both species, their types, as well as spores, and could find no differences. He had also examined a number of other specimens, previously assigned to several so-called different species of *Symphyogyna* and *Pallavicinia*, all of which he eventually placed in synonymy under *S. brasiliensis*. Three of these species, namely *S. lehmanniana*, *S. valida* and *Pallavicinia capensis*, have types which were collected in southern Africa. The following description of *S. brasiliensis*, which is illustrated with photographs, is given to draw attention to the above information.

The two Metzgerialean genera, *Symphyogyna* and *Pallavicinia* were previously placed in the family Dilaenaceae (Dum.) Warnst. by Arnell (1963) and by Schuster (1964, 1982), but this name is illegitimate (Grolle 1972). They are now classified by Grolle (1983) in the family Pallaviciniaceae Migula and are placed in different subfamilies, the Symphyogynoideae (Trev.) Schust. and the Pallavicinioideae (Migula) Grolle respectively. They are frondose liverworts, characterized by thinly winged thalli with a thicker midrib, containing a median conducting strand of elongate, tapering cells with thickened, perforated walls. The thalli are often stipitate and are either procumbent or erect; their margins are entire, dentate, undulate or lobate; the epidermal cells are ± rectangular and lack nodular thickenings and the capsules are elongated. The two genera are separated by the type of protection provided for the archegonia and young sporophyte: in *Pallavicinia* the archegonia, and after fertilization, the pseudoperianth and capsule, are surrounded by a short tubular or annular involucre; in *Symphyogyna* the archegonia are subtended by a laciniate, scale-like involucre with the margins of the latter free and directed forward, no pseudoperianth is developed after fertilization and the young sporophyte is enclosed only by the shoot-calyptra, which has a cluster of unfertilized archegonia at its tip.

Symphyogyna brasiliensis *Nees & Mont.* in Annales des sciences naturelles, Botanique sér. II.5: 67 (1836). Type: Brazil, Est. Minas Geraes, São João Batista, *Martius s.n.* (STR, lecto.).

S. lehmanniana (Mont. & Nees) Gottsche *et al.*: 483 (1846). Type: Cape Province, Table Mountain, 'in Promontorio Bonae Spei in vertice ad latus boreale montis Tabularis locis umbrosis', *Ecklon s.n.* (STR, lecto.).

S. tenuicostata Steph.: 306 (1895). Type: Tanzania, Usambara, *Holst 688* (JE, W, iso.).

S. valida Steph.: 69 (1917); syn. fide S. Arnell: 111 (1963). Type: Zululand, Eshowe, *Haakon s.n.* (JE, M, UPS, iso.).

Pallavicinia capensis S. Arnell: 177 (1954); syn. fide S. Arnell: 111 (1963). Type: Cape Province, Knysna, Gouna (not Guona) Forest, *S. Arnell 1769* (PRE, holo.!; UPS, iso.).

Terricolous, growing on damp soil; thallose, prostrate and creeping (Figures 1A; 2B), in crowded, overlying mats, bright green when fresh, rarely developing a purplish or reddish tinge along margins and over costa, linear, simple or dichotomously branched, sometimes with ventral intercalary branching, medium-sized to large, 10–20 × 2–3 mm, 280 μm thick over ventrally bulging costa, from which arise pale brownish, translucent rhizoids, smooth and mostly ± 12.5 μm wide; apex entire or with a shallow notch (Figure 1B), the two halves very slightly overlapping in centre, bearing numerous 2-celled slime papillae, ± 65 × 20 μm (Figure 1B), these also present ventrally near the apex; margins entire, undulate, without slime papillae. *Wings* translucent, unistratose,

* National Botanical Institute, Private Bag X101, Pretoria 0001.
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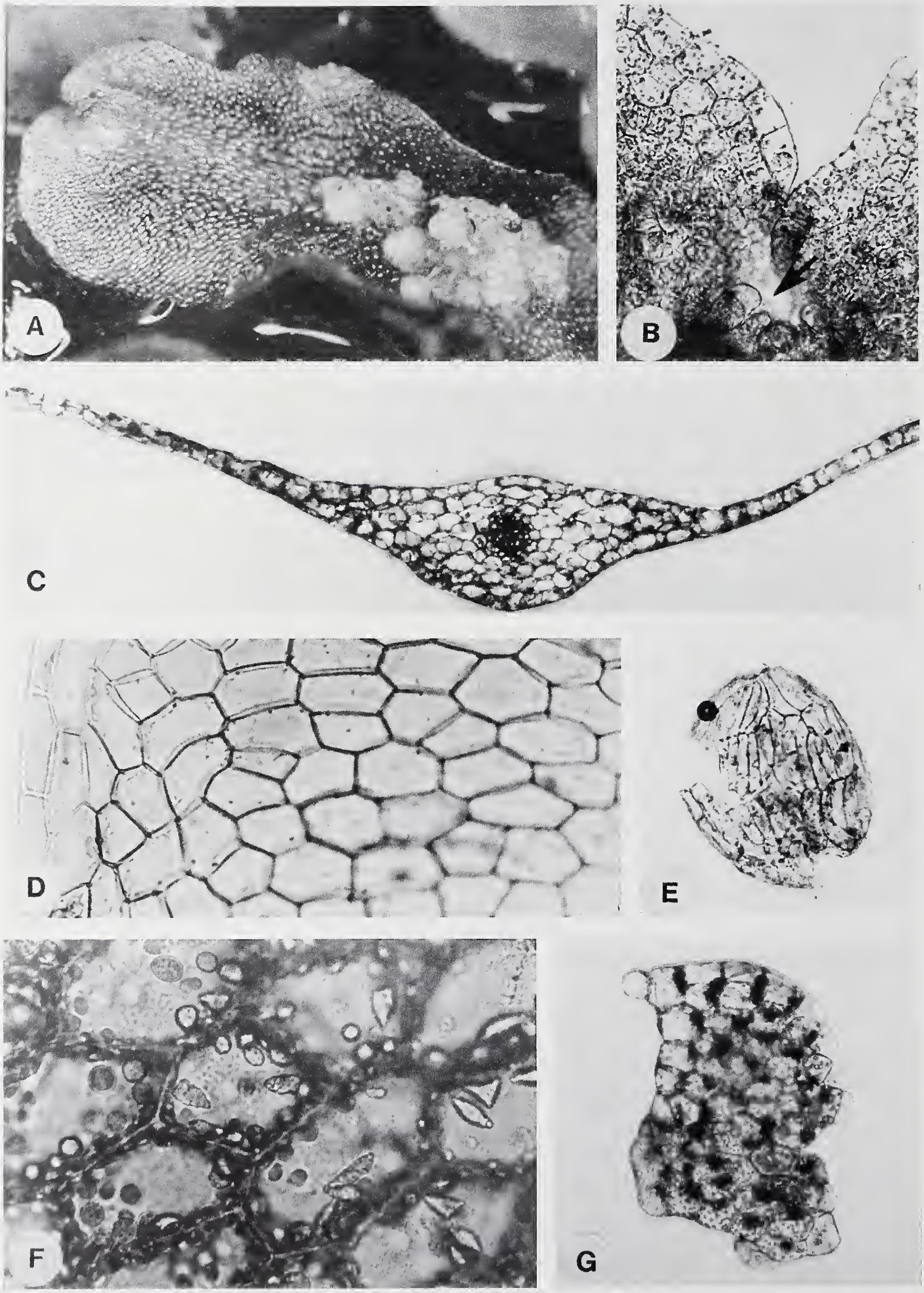

FIGURE 1.—*Symphyogyna brasiliensis*. A, male thallus with androecia; B, apical notch of thallus with slime papillae (indicated by an arrow); C, cross section of thallus showing costa with central conducting strand and unistratose lateral wings; D, marginal and laminal cells seen from above; E, antheridium; F, oil bodies and chloroplasts visible inside cells; G, scale-like involucre which partly covers antheridium. A–G, *Glen 2687*. A, × 22; B, F, × 350; C, E, G, × 87; D, × 175.

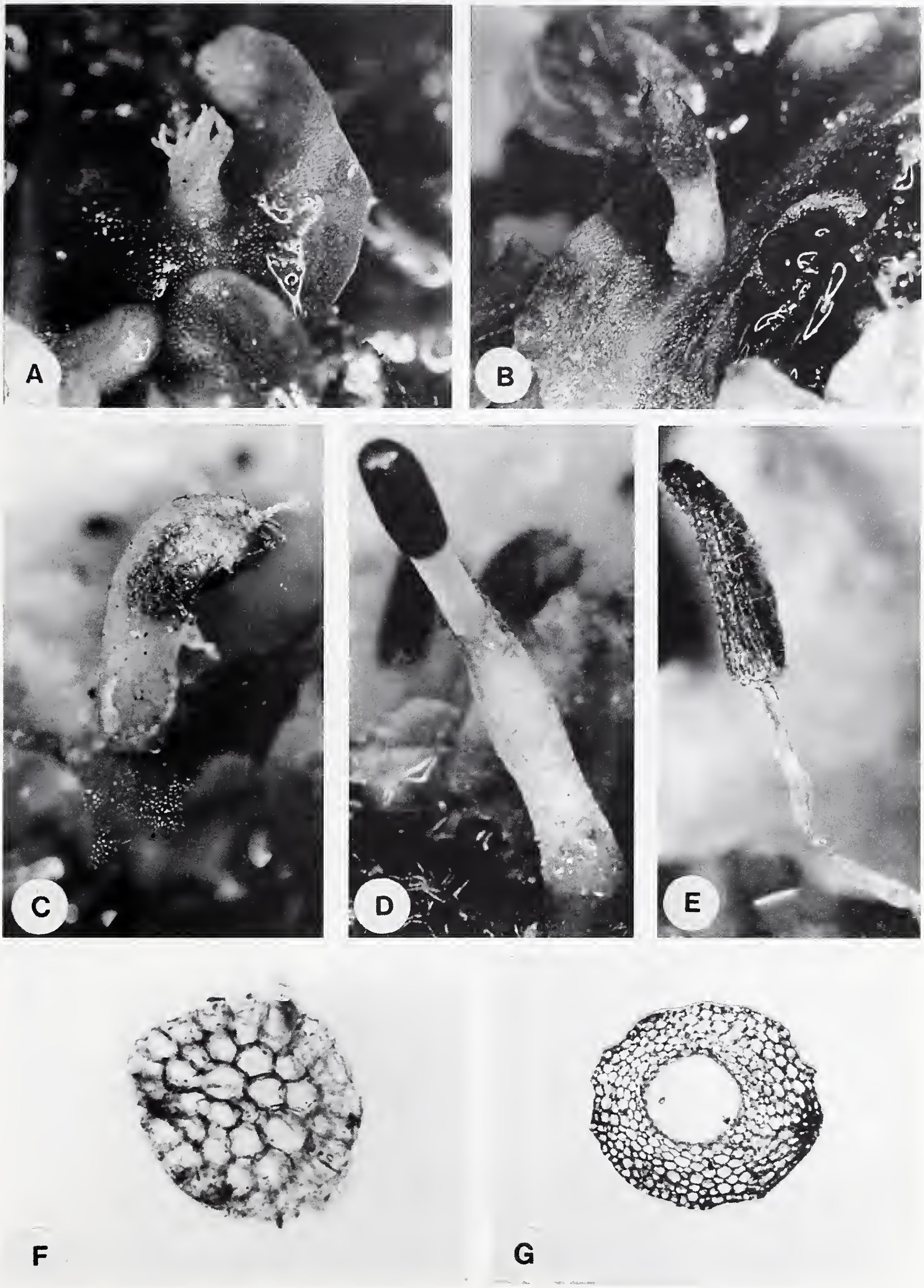

FIGURE 2.—*Symphyogyna brasiliensis*. A, female thallus with cluster of archegonia; B–E, various stages in maturation of capsule: B, C, young capsule enclosed in calyptra; D, capsule and seta emerged from calyptra; E, capsule with ripe spores and long, tenuous seta; F, cross section of seta; G, cross section through middle of shoot-calyptra. A–G, *Glen 2687*. A, B, E, × 24; C, × 34; D, × 30; F, × 110; G, × 40.

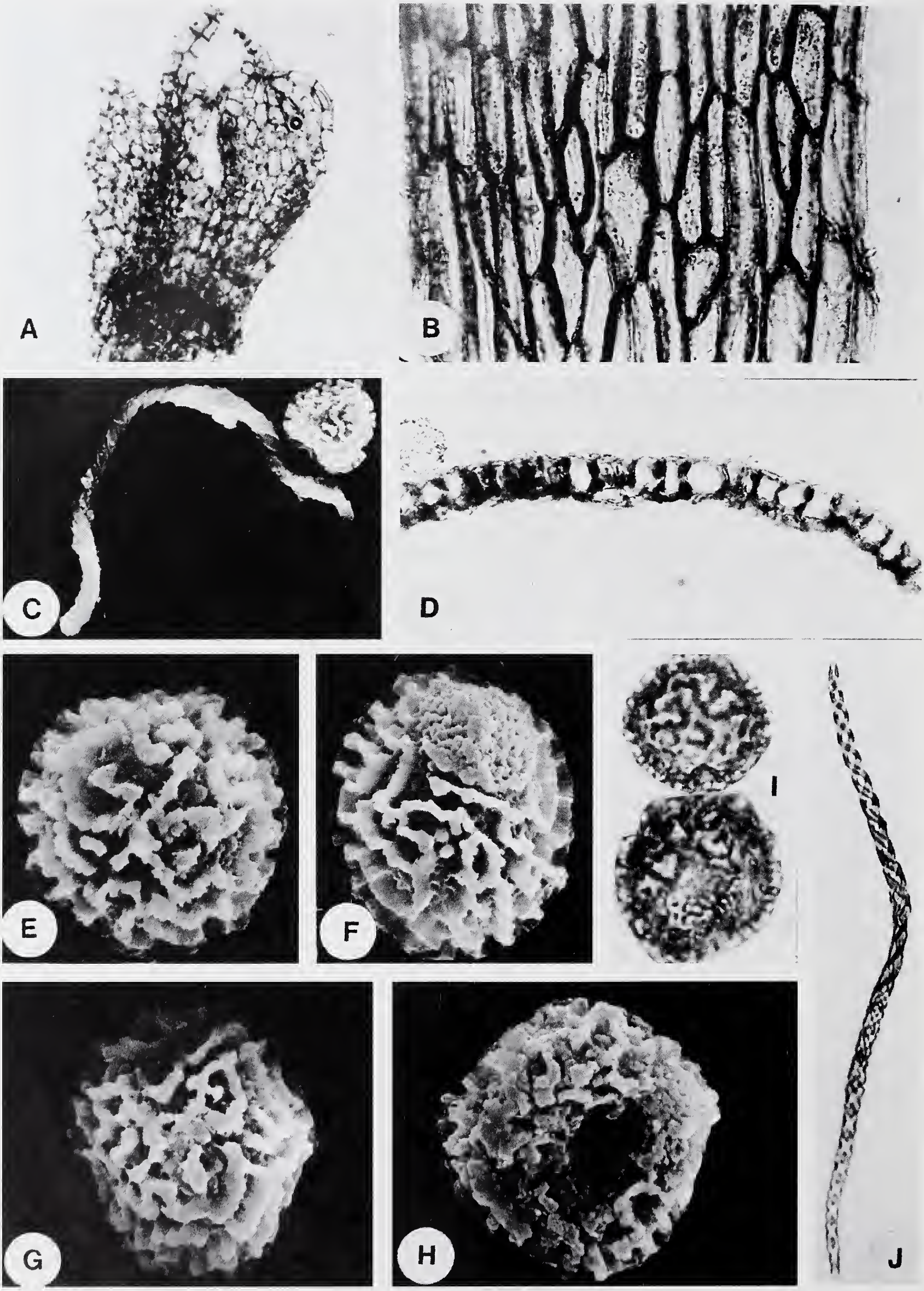

FIGURE 3.—*Symphyogyna brasiliensis*. A, laciniate scale-like involucre which subtends each archegonium; B, cells in capsule wall; C, J, elaters; D, cross section of capsule wall, only outer cells shown; E–I, spores; . A–J, *Glen 2687*. A, × 35; B, D, × 175; C, × 58; E, F, × 1750; G, H, × 1630; I, × 1000; J, × 550. C, E–H, SEM micrographs; A, B, D, I, J, LM photographs, all taken by the author.

medianly 2 or 3 cells thick, rather abruptly grading into the roughly triangular costa; outer row of cells along margin generally rectangular, ± 50.0 × 27.5 μm, otherwise cells 5- or 6-sided, 50–75 × 30.0–37.5 μm (Figure 1D) and ± 40 μm thick in section, containing numerous chloroplasts and fusiform or ± triangular oil bodies (Figure 1F). *Costa* with a central conducting strand (Figure 1C), ± 45 μm wide, brownish to purple, formed of strongly elongated, small cells, ± 10.0 × 7.5 μm, with straight, thickened walls, the enclosing cells up to 10 or 11 rows deep, hyaline, much larger, mostly 50.0 × 27.5 μm, irregular in shape, walls thin and wavy.

Dioicous. *Androecia* usually in 2 crowded (Figure 1A), more or less parallel rows over the costa and lateral to it on either side, each short-stalked antheridium (Figure 1E) partially covered by an irregularly shaped, dentate or entire, forwardly-directed, scale-like involucre (Figure 1G), ± 800 × 450 μm, its cells mostly 67.5 × 45.0 μm, with age antheridia turn yellow and cell walls of scales darken. *Gynoecia* generally one to several per frond, in acropetal succession, situated dorsally over the costa and containing several archegonia in a cluster (Figure 1A), which is subtended by a posteriorly inserted, scale-like involucre (Figure 2B), sometimes partly double toward the base, generally deeply laciniate (Figure 3A), 850–110 × 500–750 μm, its cells ± 72.5 × 50.0 μm. *Calyptra* thickening and enlarging into a fleshy shoot-calyptra, up to 3 mm long and as much as 10 cell rows or 260 μm thick in cross section (Figure 2G), with several unfertilized archegonia at the tip (Figure 2C), before it is perforated by the capsule (Figure 2D). *Capsule* cylindrical (Figure 2E), 2250 × 650 μm, opening with 4 valves, wall brown, several cell layers thick, outer cells irregularly elongate (Figure 3B), ± 200 × 20–30 μm, with cell walls evenly thickened (Figure 3D), inner cells thin-walled. *Seta* when young, erect, ± 290 μm in diameter, with ± 18 cortical cell rows and ± 16 medullary cells (Figure 2F), eventually becoming long and tenuous (Figure 2E). *Spores* light brown, ± globular, 25–30 μm in diameter, ornamentation with low, irregularly branched, short or long, curly ridges (Figure 3E, G, H), on proximal face a discrete round area with the ornamentation much more densely arranged (Figure 3F). *Elaters* bright brown, tapering to the ends, up to 195 × 7.5 μm wide in the centre, 2-spiral (Figure 3C, J).

Symphyogyna brasiliensis is widespread throughout Africa, occurring in Sierra Leone, Ghana (Jones & Harrington 1983), the Cameroons, Zaïre, Rwanda, Burundi, Tanzania, Angola, Zimbabwe, as well as on the islands of Madagascar, Mauritius, Réunion, Saint-Benoit, St Helena and Ascension (Grolle 1980; Váňa *et al.* 1979, reported as *S. lehmanniana*). In the Neotropics it is known from Mexico to Bolivia, Uruguay and Brazil (Grolle 1980).

Gradstein *et al.* (1983) reported it to be widely distributed in the tropical mountains of the two continents, Africa and South America, at altitudes between 1 500 and 3 000 m, whereas in subtropical Brazil, the Cape Province and on the Galapagos Islands it descends to near sea level.

In southern Africa it has been collected in northern, eastern, central and southern Transvaal, in Swaziland, Natal and Zululand, as well as in the southwestern and southern Cape (Figure 4).

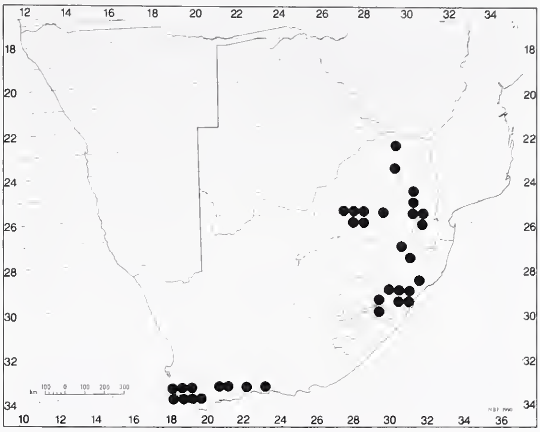

FIGURE 4.—The distribution of *Symphyogyna brasiliensis* in southern Africa.

Symphyogyna brasiliensis is terrestrial, growing on damp streambanks, along footpaths or in forested areas. It differs from the other species in the genus by its procumbent habit, by the entire margins of the thallus, by its slightly larger spore size and by its somewhat finer spore ornamentation. *S. filicum* Nadeaud from Cameroon Mountain is similar to *S. brasiliensis*, except that the small cells in the central strand are thin-walled (Jones 1990) and the spore sculpture is different. It was recently segregated as a separate genus, *Symphyogynopsis*, by Grolle in Grolle & Piippo (1986). *Symphyogyna volkensii* Steph. is more robust (Vanden Berghen 1965) than *S. brasiliensis* and has scattered slime papillae along the wing margins and different spore ornamentation (Grolle pers. comm.).

As vegetative propagation is unknown, dispersal of *S. brasiliensis* must be by long range aerial transport of its spores. Its presence on young volcanic islands would support this assumption.

SPECIMENS EXAMINED

TRANSVAAL.—2229 (Waterpoort): Soutpansberg, Lokorhela 793 Farm, ± 500 m upstream of waterfall, streambank in forest, 1 320 m altitude, (–DD), *Glen 2687* (PRE). 2329 (Pietersburg): The Downs, Pietersburg, (–CD), *Junod 4011b* (PRE); Woodbush For. Res., Magoebaskloof, on roadside embankment, (–DD), *H. Anderson CH13496* (PRE); Houtboschdorp, (–DD), *D.R.J. Van Vuuren 1478a* (PRE). 2430 (Pilgrim's Rest): Mariepskop, immediately W of dam in Klaserie River, on wet earth bank, (–DB), *Vorster 511, 575* (PRE); Mariepskop, near forestry station in riverine montane forest, on shale embankment, (–DB), *Vorster 783* (PRE). 2527 (Rustenburg): Buffelspoort, Krom River, (–CD), *Bottomley & Doidge CH3603* (PRE); Bokfontein, Farm Jacksonstuin, (–DA), *Mogg CH13173* (PRE). 2528 (Pretoria): Magaliesberg, Boekenhoutskloof, (–CB), *Mogg CH1562, CH2858* (PRE). 2529 (Witbank): Dist. Verena, 24 km E of Bronkhorstspruit, on road to Susterstroom, Farm Klipfontein, in gulley, (–CA), *S.M. Perold 452* (PRE); Klipfontein no. 87, in open glades at streamside, (–CC), *Mogg 12561* (PRE). 2530 (Lydenburg): 10 km E of Lydenburg, in road stone quarry, off Sabie/Lydenburg road, (–AB), *Rankin 53* (PRE); Rooiwal, in ravine, (–BD), *Bosman 3178* (PRE); Rosehaugh, (–BD), *T.R. Sim 7585* (PRE); Kaapsche Hoop, (–DB), *V.A. Wager 65* (PRE). 2531 (Komatipoort): Barberton, (–CC), *Hendry 2* (PRE). 2627 (Potchefstroom): Witpoortjie, near Johannesburg, (–BB), *Moss CH1465* (PRE); Witpoortjie kloof, on damp bank, (–BB), *C.S. & M. Moss CH1479* (PRE). 2628 (Johannesburg): Johannesburg, (–AA), *Edwards CH1461* (PRE). 2730 (Vryheid): Wakkerstroom Dist., Farm Oshoek, (–AD), *Glen 1676* (PRE).

SWAZILAND.—2531(Komatipoort): Horo Forest, (–CB), *V.A. Wager 92* (PRE). 2631 (Mbabane): Mbabane, (–AC), *Rodin CH3975* (PRE); Mbabane, (–AC), *Edwards CH1447* (PRE).

NATAL.—2730 (Vryheid): Scheepers' Nek, (−DC), *T.R. Sim 8231* (PRE); Vryheid, (−DD), *T.R. Sim CH1452* (PRE). 2831 (Nkandla): Eshowe, Signal Hill, (−CD), *Van der Plank CH1446* (PRE). 2929 (Underberg): 0.5 km N of Tabamhlope Police Sta., towards Draycott, on vertical to overhanging streambank, (−BA), *Glen 1693* (PRE); Rosetta, (−BD), *T.R. Sim CH1470* (PRE); 1 km beyond Sani Pass Hotel, streamlet at roadside, (−CB), *S.M. Perold 2501* (PRE). 2930 (Pietermaritzburg): Buccleuch, (−AD), *T.R. Sim CH1471* (PRE); Ndwedwe, Zwatini Kloof forest, on moist cliff, (−BD), *Strey 7757* (PRE); Pietermaritzburg, Chase Valley, (−CB), *Bews CH4466* (PRE); Zwaartkop, (−CB), *T.R. Sim CH1482* (PRE); Hilton Road, (−CB), *T.R. Sim CH1454, CH1469, CH1483* (PRE); Sweetwaters, (−CB), *T.R. Sim CH1466, CH1476* (PRE); Inchanga, at stream, (−DA), *T.R. Sim CH1451, CH1468, CH1484, CH1486* (PRE); New Germany, (−DD), *Moonsammy 21* (PRE); *Van der Byl 21 CH1460* (PRE). 3029 (Kokstad): Kingston, (−AA), *T.R. Sim CH1485* (PRE).

CAPE.—3318 (Cape Town): Table Mtn, Disa Ravine, alt 2500 ft., (−CD), *T.R. Sim CH4414* (PRE); Stellenbosch, (−DD), *Duthie CH1459* (PRE). 3319 (Worcester): Kloof off Bain's Kloof, (−CA), *Primos CH1475* (PRE); Groot Drakenstein Mts, (−CC), *Primos CH4471* (PRE); Du Toit's River bridge, at rock face next to road, (−CC), *S.M. Perold 1151* (PRE); 4 km N of Villiersdorp, Elands River road, Du Toitsberge, near waterfall, (−CD), *S.M. Perold 624* (PRE). 3320 (Montagu): warm bath at Uitvlugt, near Barrydale, (−DC), *Muir CH4103* (PRE). 3321 (Ladismith): Garcia's Pass, (−CC), *Muir CH1467* (PRE). 3322 (Oudtshoorn): George, (−CD), *H.A. Wager CH1449* (PRE), *Wager s.n., 41* (PRE). 3323 (Willowmore): Keurbooms Rivier, (−CD), *Burtt Davy 17033* (PRE). 3418 (Simonstown): Kalk Bay, (−AB), *Potts CH1473* (PRE); Gordon's Bay, Felswände südlich dem Dorfe, (−BB), *Cholnoky 386* (PRE); Kogelberg near Gordon's Bay, (−BB), *Mogg CH938* (PRE). 3419 (Caledon): Hermanus Dist., Riviera Kloof, (−AC), *Louwrens CH2893* (PRE); Voëlgat, (−AC), *Louwrens CH3715* (PRE); Mossel River, (−AD), *Potts CH4475* (PRE); Greyton Kloof, on earth bank, (−BA), *S.M. Perold 1164* (PRE). 3423 (Knysna): Knysna, Gouna (not Guona) Forest, (−AA), *Arnell 1769* (type of *Pallavicinia capensis*), *1790* (PRE); Knysna, (−AA), *Arnell 1476* (PRE); Gouna For. Res., N of Knysna, on damp earth bank at stream, (−AA), *S.M. Perold 904* (PRE).

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Morphology, evolution and taxonomy of *Wachendorfia* (Haemodoraceae)

N.A. HELME* and H.P. LINDER*

Keywords: *Dilatris*, evolution, Haemodoraceae, morphology, phylogeny, taxonomy, *Wachendorfia*

ABSTRACT

Wachendorfia Burm. is a small genus endemic to the Cape Floral Region. Four species are recognised in this study. Two species were originally described by Burman in 1757 and these were followed by numerous other descriptions of what is essentially one very variable species (*W. paniculata* Burm.). This variation is discussed and reasons are given as to why the recognition of formal infraspecific taxa is inappropriate. Formal taxonomic descriptions, distribution maps and a key to the species are provided. Rhizome morphology, leaf anatomy and pollen and seed coat structures were investigated and illustrations are provided. A cladogram was inferred and this is consistent with an ecological speciation model for the genus. The two species with the most restricted distribution (*W. brachyandra* W.F. Barker and *W. parviflora* W.F. Barker) are considered to be the most recently evolved. Features of systematic and ecological interest (e.g. floral enantiomorphy) are discussed.

UITTREKSEL

Wachendorfia Burm. is 'n klein genus endemies aan die Kaapse Floristiese Streek. Vier spesies word in hierdie ondersoek erken. Aanvanklik is twee spesies in 1757 deur Burman beskryf, en hulle is gevolg deur talle ander beskrywings van wat in wese een baie variërende spesie (*W. paniculata* Burm.) is. Hierdie variasie word bespreek en redes word verstrek waarom die formele erkenning van infraspesifieke taksons onvanpas is. Formele taksonomiese beskrywings, verspreidingskaarte en 'n sleutel tot die spesies word verskaf. Risoommorfologie, blaaranatomie en stuifmeel- en saadhuidstrukture is ondersoek en word geïllustreer. 'n Kladogram is afgelei en is in ooreenstemming met 'n ekologiese spesiasiemodel vir die genus. Die twee spesies met die mees beperkte verspreiding (*W. brachyandra* W.F. Barker en *W. parviflora* W.F. Barker) word beskou as dié waarvan die evolusionêre ontwikkeling mees onlangs plaasgevind het. Kenmerke van sistematiese en ekologiese belang (bv. enansiomorfie by die blom) word bespreek.

INTRODUCTION

Wachendorfia Burm. is a small genus (four spp.) of the Haemodoraceae (tribe Haemodoreae), restricted to the Cape Floral Region of southern Africa (*sensu* Bond & Goldblatt 1984).

The Haemodoraceae is divided into two tribes: the Haemodoreae and the Conostyleae (Geerinck 1969; Hutchinson 1973). The southern African Haemodoraceae (*Barberetta* Harv., *Dilatris* Berg. and *Wachendorfia*) are all members of the tribe Haemodoreae, which is defined by the presence of two perianth whorls, a short or absent tube and three or six stamens. The Conostyleae is represented in Australia and North America and is characterised by one perianth whorl, long, often hairy tubes, and six stamens.

The presence of arylphenalenone pigments was hypothesized by Simpson (1990) to be the most reliable synapomorphy defining the Haemodoraceae. These pigments provide the rhizomes, and probably the flowers of *Wachendorfia* and related genera, with their red component. In addition, he suggested that 1, bifurcate cymes; 2, an inferior ovary position; and 3, discoid or ovoid-globose seeds may be further synapomorphies. However, *Barberetta* does not possess a cyme (interpreted as an autapomorphy by Simpson (1990)) and a number of genera including *Wachendorfia* have superior ovaries, a reversal according to Simpson (1990). Almost all of the species (63 out of 78) and the genera (12 out of 17) are found in South America, southern Africa and Australia. The family may therefore be interpreted as being essentially Gondwanan.

Wachendorfia species have attractive yellow flowers, with a form of enantiomorphy that manifests itself in the production of both 'left-' and 'right-handed' floral forms within a population. This form of enantiomorphy is restricted to *Wachendorfia* and *Barberetta* (Ornduff & Dulberger 1978). Floral enantiomorphy has been interpreted as a mechanism to increase intermorph (and thus interplant) pollinations, ensuring effective outcrossing (Wilson 1887; Ornduff & Dulberger 1978), as a means of reducing pollen wastage or of preventing damage to the gynoecium during pollinator visits. There is, however, still much to be learnt concerning the evolutionary and ecological significance of this trait. The fact that this extremely unusual feature is most common in a small, endemic fynbos genus makes the systematic study of this group potentially fascinating. A sound taxonomic base is essential if one wishes to use the genus for exploring some of the intriguing evolutionary questions posed by the group, yet the taxonomy is at present confused, with the species limits of *W. paniculata* vague, and several possible new species unpublished. In this study we hope to come to an understanding of species delimitation within the genus, and increase our knowledge of the ecology and possible evolutionary history of the species, with a view to highlighting areas of potentially rewarding systematic study.

METHODS

Plant morphology

Gross morphology was determined by field observation and examination of extensive material lodged in BOL,

* Bolus Herbarium, University of Cape Town, Rondebosch 7700.
MS. received: 1991-07-09.

NBG, PRE, SAM and STE. These specimens have all been provided with determinavit labels. Rhizome and culm (annual flowering stem) morphology was investigated using fresh plants at different stages of development. Details were observed with a Wild stereo dissecting microscope. Thin sections were hand-cut with a scalpel and then stained with iodine to investigate the presence of starch.

Pollen morphology

Pollen was taken from either herbarium specimens or from live material collected in the field. For both light microscopy (LM) and scanning electron microscopy (SEM), pollen was acetolysed according to the method of Erdtman (1960). Half the acetolysed pollen was mounted in glycerine on a slide and sealed with wax for light microscopy. The other half was mounted on aluminium stubs and sputter coated with Au/Pd and examined in a Cambridge S200 SEM at 10kV. LM photographs using differential interference contrast and oil immersion were taken on a Zeiss Axioskop photomicroscope using Ilford FP4 film. Pollen measurements were made using engraved stage micrometer units in conjunction with an eyepiece scale.

Pollen sources, vouchers in BOL

Wachendorfia brachyandra: Cape Point, *Salter 8718.*
W. graminifolia: Constantia Nek, *Barker 170.*
W. paniculata: Hermanus, *Burman 936*; Mamre, *Esterhuysen 5244*; Waaihoek Peak, *Esterhuysen 8283.*
W. parviflora: Clanwilliam, *Le Roux 2626.*
W. thyrsiflora: Humansdorp, *Fourcade 2436.*
Dilatris corymbosa: Cape Point, *Pillans 4589.*
D. pillansii: Cape Point, *Salter 7902.*

TABLE 1.—The characters, character states and coding used in the cladistic analysis. The first state is coded 0, the second, 1 and the third, 2

Gross plant morphology:
1 Plant height greater than 1 m/less than 1 m
2 *Corm length greater than 30 mm/less than 30 mm
3 Leaf length greater than 500 mm/less than 500 mm
4 Leaf width greater than 50 mm/less than 50 mm
5 Leaves glabrous/with short and dense indumentum
6 Bracts scarious/herbaceous
7 Max. peduncle length greater than 100 mm/less than 100 mm
8 Cilia on the petal margins present/absent
9 Ratio stamen to tepal length: greater than 0.6/less than 0.6
10 Average minimum tepal width greater than or equal to 6 mm/ less than 6 mm
11 Max. tepal length greater than 20 mm/less than 20 mm

Leaf anatomical characters:
12 *Leaf chlorenchyma pallisade two cells wide/one cell wide/ absent
13 Sclerenchyma cap on the vascular bundles well developed/ poorly developed or absent
14 Mucilage canals along leaf margins/scattered in mesophyll
15 Cuticle thick/thin
16 Lignification of epidermis light/heavy
17 Guard cell with one lip/two lips
18 *Subsidiary cell kidney-shaped/rectangular
19 Cortical cells unlobed/lobed

Pollen characters:
20 Sulcus to verrucae distance greater than 10 μm/less than 10 μm
21 Exine sculpturing verrucate/reticulated

Seed characters:
22 *Seed shape spherical/ovate/disk-shaped
23 Seed diameter greater than 4 mm/less than 4 mm
24 Epidermal cell shape rectangular/irregular

Chemical characters:
25 Colour of pressed flowers purple/orange

* cladistically informative characters.

TABLE 2.—Cladistic character codes for each species. Characters arranged according to Table 1, missing data codes as 9

	Characters				
Taxa	5	10	15	20	25
Dilatris	11110	01999	10000	01019	12110
W. thyrsiflora	00000	01000	02111	01000	01001
W. paniculata	10119	00900	01011	01101	00100
W. brachyandra	11110	01110	11011	01101	00100
W. parviflora	11111	19101	11011	11101	00100

Seed morphology

Seeds were taken from herbarium material or from material collected in the field. Seeds were air dried, mounted on aluminium stubs, and sputter coated with Au/Pd and examined in a Cambridge S200 SEM at 5kV.

Seed sources, vouchers in BOL

Wachendorfia brachyandra: Kirstenbosch, *NBG s.n.*
W. paniculata: Mamre, *Esterhuysen 5244*; Kommetjie, *Helme 7*; Boulders beach, *Leighton 34*; Tulbagh, *Leighton 37.*
W. parviflora: Kirstenbosch, *NBG s.n.*
W. thyrsiflora: Kirstenbosch, *NBG s.n.*
Dilatris ixioides: Pakhuis Pass, *Esterhuysen 3165*
D. viscosa: Tulbagh, *Leighton 40.*

Leaf anatomy

Fresh material used for the anatomical study was collected from plants in the field, and fixed and preserved in Kew Cocktail (16:16:1:1 = distilled water:EtOH:formalin: glycerine). Fresh material was favoured because cellular constitution is more easily observed and is less likely to show distortion than dried and reconstituted material. Sections were sledge microtomed to a thickness of 25 micrometers and stained in Alcian Blue and Safranin (lignin stain and counterstain) for 30 minutes (Tolivia & Tolivia 1987). Sections were then washed in distilled water and dehydrated in an alcohol series before mounting in DPX.

Epidermal leaf scrapes were mounted in Hoyer's solution (Anderson 1954), which results in cleared, permanent mounts. These slides were then used for the examination of leaf surface features such as stomata, cell shape and hair structure.

Cladistic analysis

A cladistic analysis was performed on the four species of *Wachendorfia* and the outgroup, *Dilatris*. Twenty-five characters were investigated for use in the analysis, but only four proved to be cladistically informative (Table 1), because their evolutionary polarity could be determined and they occur in more than one species. A list of character codes is given in Table 2. The most parsimonious cladogram, that is the diagram that requires the least number of character changes, was determined using Hennig86 (Farris 1988), and PAUP vers. 2.4 (Swofford 1985) was used to calculate the patristic distances for each species and to optimize the characters on the cladogram.

Dilatris was used as the outgroup because it has many morphological features in common with *Wachendorfia*. The only other possible outgroup is *Barberetta*, but no good material was available of this genus. Ornduff (1979) suggested that, on the basis of chromosome numbers, *Wachendorfia* and *Barberetta* (both with n=15) are more closely related to each other than either is to *Dilatris* (n = ±19–21). De Vos (1956), however, suggested that *Wachendorfia* and *Dilatris* are closely related, based on embryological studies, but she unfortunately did not investigate *Barberetta* which possesses an unusual floral structure for the Haemodoraceae, namely, a simple raceme, unlike *Wachendorfia* or *Dilatris*, which have helicoid cymes. Evidence therefore exists both for and against choosing *Dilatris* as the outgroup for *Wachendorfia*, although the case for choosing *Barberetta* could be stronger. Simpson (1990) showed that on available information, *Barberetta* is the sister taxon of *Wachendorfia* and that these two together are the sister group of a clade consisting of the New World genera *Schlekia* and *Pyrrorhiza*: *Dilatris* was viewed as more distantly related. However, as the outgroup need not be the sister taxon of the study group (Watrous & Wheeler 1981; Maddison *et al.* 1984), we used *Dilatris* as the outgroup. It should be borne in mind that this may result in a poorer resolution of the phylogeny than when the sister taxon is used as the outgroup.

TAXONOMY

Historical background

The earliest description of a *Wachendorfia* was by Plukenet in 1700 and he named these specimens from the Cape of Good Hope *Erythrobulbus*. These descriptions were probably based on material collected by Oldenland. Forty years later Breyne (1739) illustrated and described what was clearly a *Wachendorfia* under the name *Asphodelus*. Hendrik Oldenland, the Superintendent of Simon van der Stel's Company Garden in Cape Town during the period 1691–1699, made some of the earliest collections in the vicinity of Cape Town. This collection of notes and plants was neglected for many years, until Johannes Burman published the first post-Linnean descriptions of *Wachendorfia* in his monograph of the genus (Burman 1757). Two species, *W. thyrsiflora* Burm. and *W. paniculata* Burm., were accurately described. In 1758, Loefler unwittingly applied the name *Wachendorfia* to what is now known as *Callisia* Loefl. (Commelinaceae). The name *Wachendorfia* commemorates E.J. van Wachendorff, who was Professor of Botany and Chemistry at Utrecht during the 18th Century (Jackson 1987).

Thunberg visited the Cape between 1772 and 1775, and made extensive collections, which included specimens of *Wachendorfia*, some of which were described by Linnaeus (filius) as *W. graminifolia* in his *Supplementum plantarum* (1781). Thunberg, in his *Prodromus* (1794) and *Flora capensis* (1811), described *W. graminea*, *W. tenella* and *W. hirsuta*. Salisbury added *W. elata*, *W. humilis*, *W. pallida* and *W. brevifolia* in 1796, whereas two more names were proposed in the 19th century. Baker (1896) relegated most of these above-mentioned names to the rank of variety or synonym of *W. thyrsiflora* and *W. paniculata*.

The genus was then virtually ignored for 120 years, until Barker (1949) published two new species, *W. parviflora* W.F. Barker and *W. brachyandra* W.F. Barker. Although these species have a more restricted range and are perhaps less common than the initial two species, it is surprising that such striking plants could go undetected for so long.

Wachendorfia *Burm.*, in Wachendorfia: 2 (1757); Linnaeus: 864 (1759); Bak. 6: 1 (1896); W.F. Barker: 206 (1950); Geerinck: 58 (1969); Dyer: 946 (1976). Type species: *W. thyrsiflora* Burm.

Wacchendorfia Burm.f. (sphalm.) (1768).
Wachendorffa Cothen. (orth. var.) (1790).
Pedilonia Presl (1829).

Pre-Linnean synonyms:

Erythrobulbus Pluk.: v 5 (1700).
Asphodelus Breyne: t. 22 (1739).

Perennial, rhizomatous herbs 0.1–2.5 m tall; leaves usually annual (one species perennial); annual culms develop from a rhizome. *Rhizome* fleshy, bright red, irregular to ovoid, nodes three, opposite, each with an axillary bud, apical bud producing the culm; new rhizome produced annually from an axillary bud, 1–3 old ones remaining attached; roots thin, adventitious, clustered around node between old and new rhizomes; old rhizome leaf bases forming a tunic around rhizome; ramets often formed. *Leaves* erect or spreading, linear, lanceolate, or falcate, firm in texture, always longitudinally plicate, simple and entire, glabrous to hirsute, green to yellow-green, 0.1–0.9 m long; lower leaves sheathing at base of culm; rhizome leaves 3, stem leaves variable in number, lowest two stem leaves amplexicaul and opposite, leaves above spirally arranged and not amplexicaul. *Culm* annual; 0.1–2.5 m tall. *Inflorescence* a lax deltoid to dense cylindrical panicle; peduncles herbaceous, terete to angular, very short to long (up to 0.25 m), near vertical, or spreading; main axis covered in short hairs, pilose at base, glandular nearer apex. *Bracts* erect or recurved, herbaceous or scarious, acute, usually hairy, older scarious bracts often recurved. *Flowers* with tepals 6, borne in 2 whorls, subequal, spreading, oblong; lower 3 free, upper 3 united at base with small dark and light markings near base; two open spur-like nectaries produced from the bases of outer upper tepal and 2 adjacent inner tepals; outer segments hairy on outside, especially central upper tepal; yellow to pale apricot. *Stamens* 3, opposite the inner tepals; filaments free, filiform, declinate, the upper two pendulous, the lowest turning sideways opposite style; anthers ovate-sagittate, two-celled, dehiscing longitudinally, introrse, usually included, 0.2–3.0 × 0.5–1.0 mm; pollen boat-shaped, monosulcate, heteropolar, with a verrucate, two-layered exine. *Ovary* superior, pubescent, 3-locular, 1 ovule per locule, axile placentation; style filiform, bent sideways (left or right in any one plant), in same direction as one of the stamens; stigma minute, capitate. *Fruit* an acutely 3-lobed capsule, dehiscing loculicidally, usually glandular, wider than tall, pubescent. *Seeds* 1 per locule, spherical to ovoid, densely hairy.

Key features of the genus

Perennial herbs, three of the four species with annual leaves. Annual flowering stems (culms). *Perennial rhizome* with red sap. *Leaves* lanceolate, linear or falcate, simple, longitudinally plicate, entire. *Inflorescence* a panicle. *Flowers* zygomorphic, yellow, with right- and left-handed forms. *Ovary* 3-locular, locules uni-ovular. Confined to the fynbos biome.

Key to the species

1a Perianth segments narrow, 3–6 mm broad; bracts herbaceous, all erect; leaves usually as long or longer than culm; plants usually short (less than 0.25 m tall) .... 4. *W. parviflora*
1b Perianth segments broad, 5–18 mm wide; bracts scarious or submembranous, the upper usually recurved; leaves usually shorter than culm; plants usually tall (greater than 0.25 m tall):
2a Stamens and style about half the length of the tepals, clustered .... 3. *W. brachyandra*
2b Stamens and style from two-thirds to nearly as long as the tepals, spreading:
3a Plant tall (over 0.6 m); inflorescence dense, cylindrical; leaves broad (greater than 15 mm wide), glabrous, perennial .... 1. *W. thyrsiflora*
3b Plant short (usually below 0.6 m); inflorescence variable, lax to very dense panicle; leaves narrow (usually less than 20 mm broad), glabrous to hairy, annual .... 2. *W. paniculata*

1. **Wachendorfia thyrsiflora** *Burm.* in Wachendorfia: 3 (1757). Thunb.: 306 (1811); Bak. 6: 1 (1896); W.F. Barker: 206 (1950). Type: *Oldenland s.n.* (?G, not seen); iconotype: Burm.: 13, figs 1 & 2 (1757).

W. elata Salisb., Prodr. 45 (1796).

Pre-Linnean synonym:

Asphodelus latifolius Breyne: t. 22 (1739).

Rhizomatous perennial herb; 0.6–2.5 m tall. *Rhizome* up to 150 mm long, irregular, usually cylindrical, sheathed by overlapping leaf bases; rooting from nodes. *Leaves* perennial, erect, lorate to lanceolate, deeply plicate, firm, glabrous, usually shorter than the flowering stem, up to 900 × 80 mm; younger plants with leaves less than 50 mm broad. *Leaf anatomy*: palisade layer not distinct; cuticle with variable lignification; sclerenchyma caps poorly developed; subsidiary cells kidney-shaped; mucilage canals large. *Culm* up to 2.5 m tall, stout (up to 15 mm diameter near base), erect, densely pilose at base (hairs up to 4 mm long) running into short (1 mm long) glandular hairs near apex. *Inflorescence* a dense cylindrical panicle, up to 0.6 × 0.2 m. Peduncles many, short (up to 100 mm), regularly spaced on distal half of axis. Younger plants often more laxly branched; seldom more than 7 pedicels per peduncle; no secondary peduncles. *Bracts* lanceolate, scarious, recurved, persistent, 10–40 mm long. *Tepals* bright yellow, nectar guides on base of upper 3 tepals light to dark; all slightly spathulate; 12–28 × 8–14 mm; outer adaxial tepal narrower and shorter than the rest, slightly recurved; upper 5 tepals overlapping, leaving lower tepals somewhat isolated; tepals sometimes fringed with orange cilia. *Stamens*: filaments $^3/_4$ tepal length, 15–20 mm long, spreading; anthers 1.2–2.0 × 0.5–1.0 mm. *Gynoecium*: ovary yellowish, 2–3 × 1–2 mm; style 13–18 mm long. *Fruit* a 3-angled capsule, 10 × 7–10 mm. *Seed* large, up to 5 mm long, oval or kidney-shaped; dense microscopic blisters (1.5 μm) on seed hairs. *Chromosome number*: n=15 (Ornduff 1979).

Flowering time: beginning of September to end of November, occasionally to mid-January, with a peak in September and October.

Distinguishing features: large size; marshy habitat; large yellow flowers with long spreading stamens; inflorescence a dense, cylindrical panicle; peduncles short.

Distribution and habitat: *W. thyrsiflora* is a widespread species, occurring from as far north as the Olifants River valley between Citrusdal and Clanwilliam, south to the Cape Peninsula, inland to the Franschhoek Mountains, and along the south coast and associated mountain ranges as far east as Humansdorp (Figure 1). This species is more of a habitat specialist than any of the other species, and is confined to permanently moist sites, especially along streams and in seepages. The species has a wide altitudinal range, varying from about 5–±1 200 m a.s.l.

Status: locally abundant, often dominant in marshes. Some populations are very small and may be declining due to afforestation or weed infestation. The populations in mountain fynbos are generally stable.

Vouchers: *Leighton 1353* (BOL); *Levyns 3368* (BOL); *Liebenberg 7923* (PRE); *Pillans 8086* (BOL).

2. **Wachendorfia paniculata** *Burm.* in Wachendorfia: 11 (1757). Sims: t. 616 (1803); Thunb.: 307 (1811); Bak. 6: 1 (1896); W.F. Barker: 206 (1950). Type: *Oldenland s.n.* (G?, not seen); iconotype: Burm.: 15, fig. 3 (1757).

W. graminifolia L.f.: 101 (1781). *W. graminea* Thunb.: 309 (1811) nom. illeg. Type: near river at Drakenstein. *Thunberg 1242* (UPS, lecto. –BOL, microfiche!).

W. hirsuta Thunb.: 308 (1811); Sims: t. 614 (1803). Type: sand fields between Swartland and Saldanha Bay. *Thunberg 1243* (UPS, holo.–BOL, microfiche!).

W. tenella Thunb.: 308 (1811). Type: between Langevlei and Heerenlogenment. *Thunberg 1246* (UPS, holo. –BOL, microfiche!).

W. brevifolia Solander ex Ker-Gawl. (1809). Type: in the Banksian Herbarium (BM).

W. herbertii Sweet: 400 (1826), based on *W. paniculata* var. β Herbert (1826). Specimen from the Cape of Good Hope, flowering at Spofforth in July. Iconotype: Botanical Magazine 53: t. 2610 (1826), here designated.

Rhizomatous perennial herb; 0.1–0.9 m tall. *Rhizome* ovoid, up to 50 mm in diameter, appearing tunicate when dry. *Leaves* annual; narrowly lanceolate or linear to broadly falcate, erect or spreading, dull green to yellow-green, glabrescent to hairy, 3-nerved; 0.1–0.7 × 5–(20)–35 mm. *Leaf anatomy*: palisade layer one cell thick; cuticle with intermediate lignification; sclerenchyma cap development variable; subsidiary cells rectangular; mucilage canals small. *Culm* occasionally up to 1 m tall, slender to robust (3–15 mm diameter), erect, covered with short, dense simple hairs. *Inflorescence* a lax to dense racemose panicle, composed of 5–20 scorpioid cymes, each cyme bearing 1–7 flowers. Peduncles variable in number and length, longer at the base (may be branched again to form a secondary peduncle), up to 0.4 m long, slender to robust; pedicels short (less than 100 mm). *Bracts*

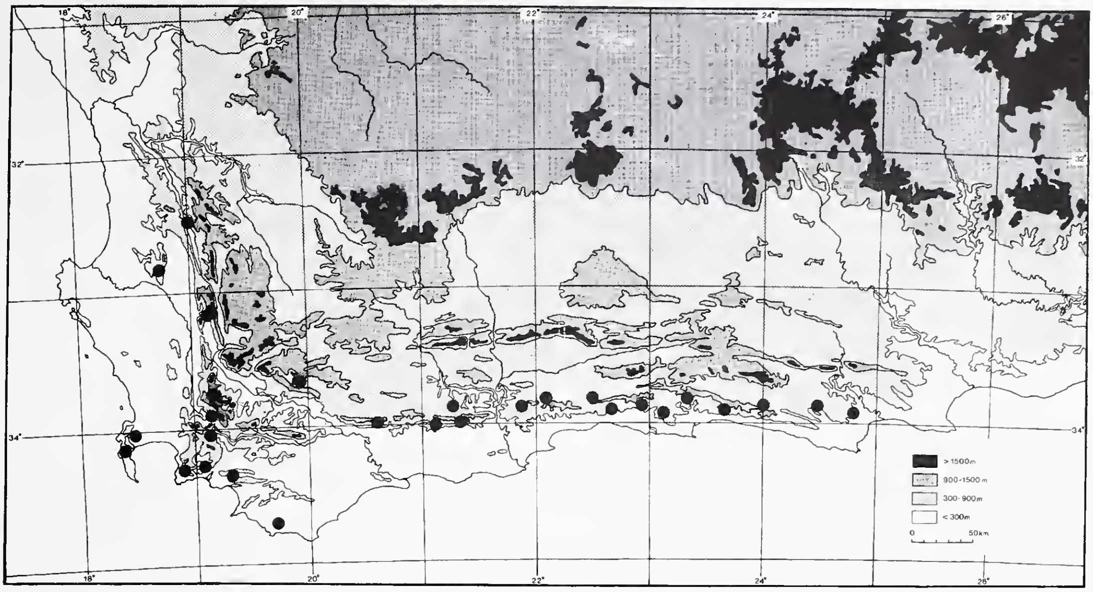

FIGURE 1.—Distribution of *W. thyrsiflora*.

scarious (often submembranous when fresh), often recurved, especially when old, 5–50 mm long, veined, long-acuminate, pilose, partly sheathing. *Tepals* apricot, yellow, or orange; slightly scented; 13.0–(21.0)–31.0 × 4.0–(10.0)–16.0 mm; inner abaxial tepal often slightly broader than the rest; outer adaxial tepal shorter, narrower, recurved; margins sometimes fringed with short cilia. *Stamens* from two-thirds to three-quarters the tepal length, spreading; anthers 2–3 × 0.8–1.0 mm. *Gynoecium*: style 15–22 mm long, as long as shortest tepal. *Fruit* an acutely three-lobed capsule; 10 × 5 mm. *Seed* spherical, coarsely pilose, brown, 2 mm in diameter. *Chromosome number*: n=15 (Ornduff 1979). Figure 2.

Flowering time: August to December, very rarely to early February (high altitude), with most records from September to November.

Common name: rooikanol or spinnekopblom.

Distinguishing features: plants from 0.15–0.80 m tall; bracts scarious when mature; stamens and style spreading, from two-thirds to three-quarters the length of the tepals; tepals broad; leaves usually shorter than the flowering stem.

Nomenclatural notes: according to Savage (1945) there is a specimen of *Wachendorfia* in the herbarium of the Linnean Society, annotated by Burman as '*Wachendorfia paniculata*'. As the Burman herbarium is generally thought to be in the Delessert Herbarium at Geneva (Stafleu & Cowan 1976) further investigation would be required to determine where the type of the name is housed.

The types of Linnaeus the Younger are mostly housed in the herbarium of the Linnean Society. However, there

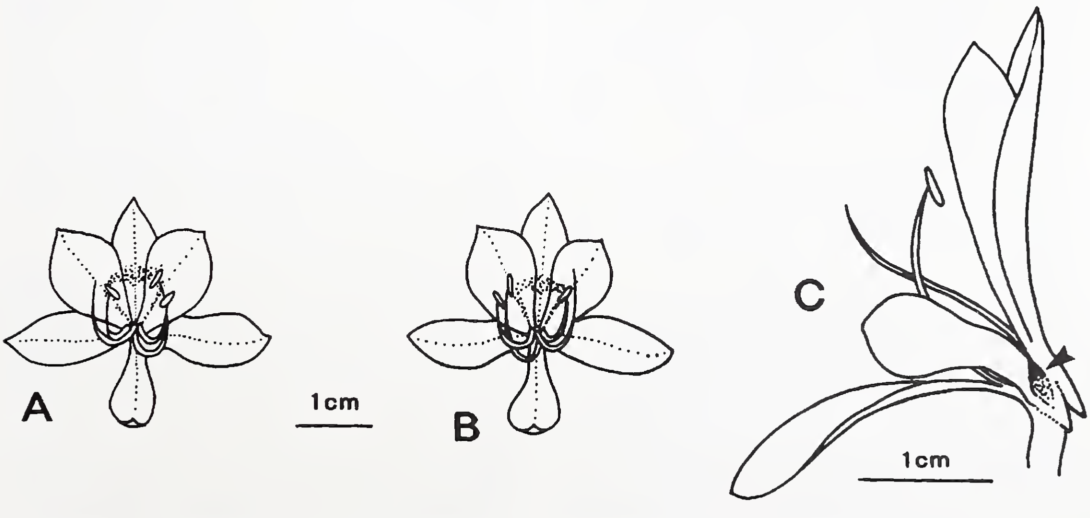

FIGURE 2.—*W. paniculata* flower structure. A, left-handed flower (stigma deflected to left); B, right-handed flower (stigma deflected to right); C, side view showing large perianth-aperture (arrowed).

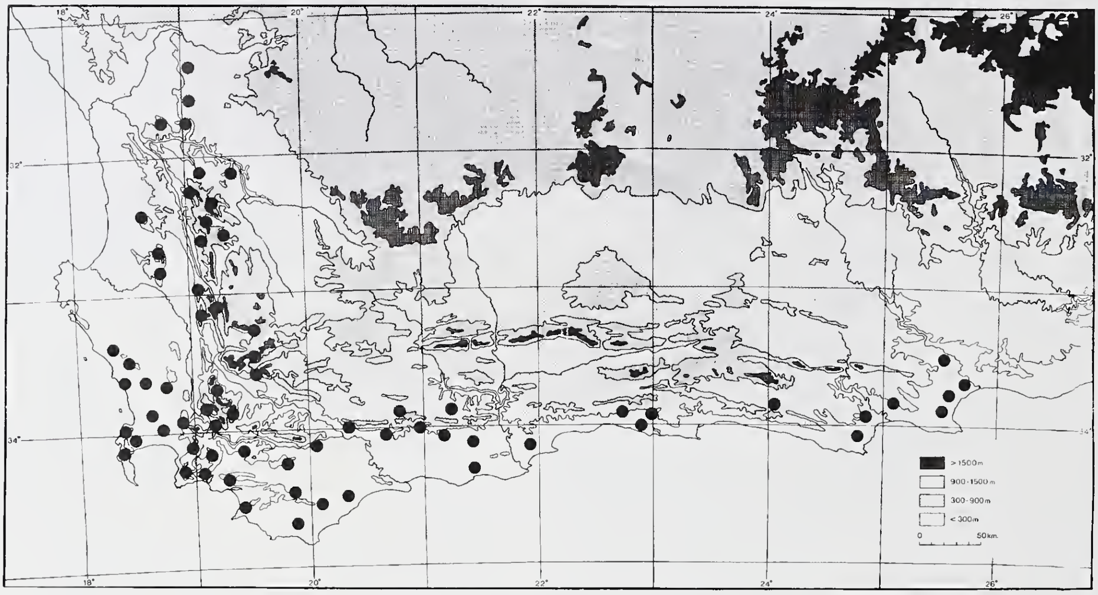

FIGURE 3.—Distribution of *W. paniculata*.

is no material of *W. graminifolia* (Savage 1945), whereas there is a specimen annotated as such by Thunberg at Uppsala. This may well be the type material, but can in the absence of further information only be designated as a lectotype.

Distribution and habitat: this is the most widespread species, ranging from Nieuwoudtville to Port Elizabeth (Figure 3). It is ubiquitous in the fynbos biome, and is found mainly on soils derived from Table Mountain Sandstone, although it has also been recorded from areas with granitic soils, alluvial sands, and clayey soils derived from Malmesbury shales. The species is found from sea level to about 1 700 m.

W. paniculata grows in mesic and dry mountain fynbos, lowland fynbos on acid or alkaline soils, renosterveld, and strandveld. It is most common in younger vegetation (less than 10 years since last fire), probably because it favours less dense vegetation. The species does not require permanent moisture and can be found in areas ranging from seasonally dry sands to permanently moist shales. This wide ecological tolerance is certain to be one of the major reasons for the success of the species.

Status: locally abundant, but usually varies from sparse to common. This species is unlikely to become endangered in the near future due to its wide distribution, varied habitats, and ability to thrive in disturbed (even ploughed) sites.

Variation within the species: *W. paniculata* is exceptionally variable with respect to plant size, leaf hairiness and shape, and flower size and structure. This has resulted in the large number of synonyms for this species.

Barker (1950) resurrected *W. graminifolia* L.f. as a segregate of *W. paniculata*. However, there is a continuum of variation in all traits mentioned by Barker as reliable discriminators, for example, perianth length, plant robustness, leaf hairiness and width. In addition, specimens show combinations of characters which make the separation of two species, based on these characters, futile, e.g. a plant may be robust and have tepals 25–30 mm long (both *W. graminifolia* characteristics), as well as narrow, hairy leaves (both *W. paniculata* characteristics). The various combinations are endless. For these reasons we do not think that *W. graminifolia* can be separated from *W. paniculata*.

An extensive review of all available herbarium specimens showed that there is neither temporal nor geographical separation between the 'varieties'. In addition, the chromosome number is constant for specimens from a wide geographical range, and exhibiting a wide range of morphological variation (Ornduff 1979). This evidence supports the idea that *W. paniculata* and all plants closely resembling it represent a single species. This variation in *W. paniculata* should somehow be recognised. However, the variation is too continuous to recognize formal taxa, and Rosendahl's (1949) comment probably applies here: 'some authors when dealing with highly polymorphous groups seem to feel that it is necessary to take account of all variants that can be distinguished and fit them into a formal scheme. The trouble with this procedure is that in attempts to set up a series of units of descending rank, a point of diminishing returns is soon reached, beyond which confusion rather than clarification results. Such schemes may have something to commend them in theory but not in practice'. The alternative is to recognize informal forms.

Stuessy (1990) defines 'form' as 'specimens with small genetic variations, not geographically correlated, and often growing with more 'typical' plants'. Subspecies and varieties apply only to allopatric taxa, and the variation within *W. paniculata* should thus be described as forms.

Form 1: this form has been recorded from Kleinmond in the east, north to Mamre, and south to the Cape Peninsula, and is characterised by large tepals fringed with dark cilia. There is continuous variation for this and other characters in the plants, and the distinctness of the morph as a whole is doubted.

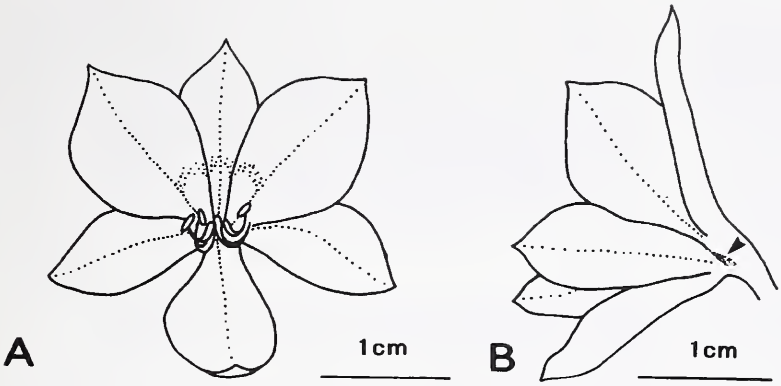

FIGURE 4.—*W. brachyandra* flower structure. A, right-handed flower illustrating clustered stamens and style characteristic of species; B, side view showing small perianth aperture (arrowed).

Form 2: specimens from the mountains between Ceres and Pakhuis Pass are frequently very tall, with extremely lax panicles and long, thin leaves. This form does have a degree of environmental and geographical correlation, which suggests that it might be viewed as a subspecies (allopatric, genetically similar). However, the form is not strictly allopatric as the typical form of *W. paniculata* is known to occur in the area and for this reason we would not recommend the use of a formal subspecific rank for this taxon.

Form 3: dwarf specimens with very narrow, hairy leaves can often be found growing together with more 'typical' forms, for example in the hills above Glencairn and Simonstown.

Vouchers: *Barker 169, 1097* (NBG); *Lewis in BOL 22263* (BOL); *Pillans 9138* (BOL); *Stokoe 818* (BOL); *Wolley Dod 526* (BOL).

3. **Wachendorfia brachyandra** *W.F. Barker* in Journal of South African Botany 15: 41 (1949); W.F. Barker: 207 (1950). Type: Cape Peninsula, Kirstenbosch, *Barker 1096* (NBG, holo.!).

Rhizomatous perennial herb, 0.10–0.65 m tall. *Rhizome* small, globose to ovate-oblong, 5–20 mm diameter. *Leaves* annual, erect or spreading, linear to lanceolate, often falcate, glabrous, dark green to yellow green, up to 700 × 35 mm. *Leaf anatomy*: palisade layer poorly defined, consisting of one or two cells; cuticle lightly lignified; sclerenchyma cap development variable; subsidiary cells rectangular; mucilage canals small. *Culm* about 3 mm in diameter, covered in short glandular hairs, seldom branched to form secondary peduncles; usually less than 0.4 m long. *Inflorescence* a lax panicle with 6–17 flowers per peduncle; peduncles and pedicels slender; peduncles short near tip of axis, a few much longer at the bottom (up to 0.2 m long). *Bracts* mostly scarious, oblong ovate acuminate, almost sheathing, not recurved lower down, up to 80 mm long; densely pilose. *Tepals* light apricot yellow, the markings dark; 12–20 × 4–14 mm; outer adaxial tepal smaller than the others, only slightly recurved; cilia seldom present on tepal edges. *Stamens* clustered, not spreading, half as long as tepals, 6–14 mm long; anthers 2.0–2.5 × 0.5–1.0 mm. *Style*: short, not much curved sideways, 7–12 mm long. *Fruit* a 3-lobed, dry capsule broader than long, 5 × 8–10 mm, carpels obtuse. *Seeds* spherical, coarsely hairy, 2 mm diameter. Figure 4.

Flowering time: late August to early December, with a peak in September and October.

Distinguishing features: stamens and style short, half the length of the tepals, clustered; inflorescence lax; tepals pale yellow-apricot.

Distribution and habitat: this species has the most restricted range of all the species, and is confined to the extreme southwestern Cape (Figure 5). It is undoubtedly undercollected, and is known from altitudes ranging from 50–±600 m on either sandstone or granite derived soils. The species seems to favour damp sites, often growing in partial shade in forest margins, or in seeps and drainage lines in fynbos. It is also commonly found in recently burnt fynbos areas, and will persist for many years in a fairly open habitat (e.g. herbaceous margins of forests).

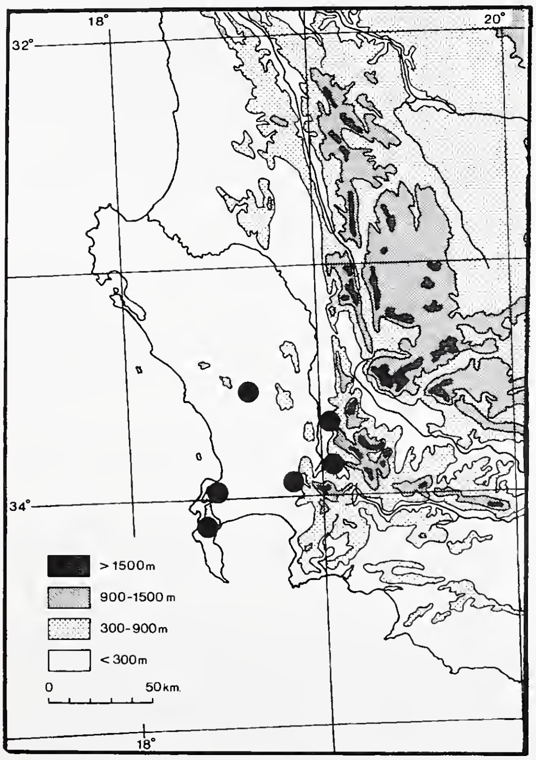

FIGURE 5.—Distribution of *W. brachyandra*.

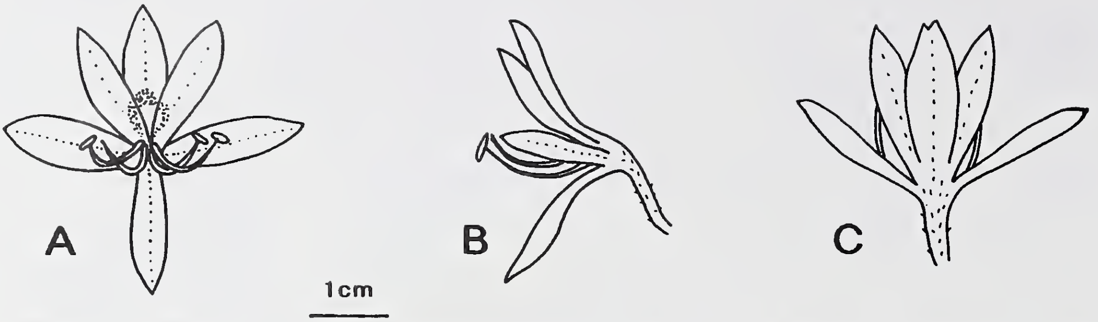

FIGURE 6.—*W. parviflora* flower structure. A, front view of left-handed flower showing narrow tepals characteristic of this species; B, side view; C, rear view.

Status: locally common, but with a sparse, scattered distribution. Due to the nature of its habitat, *W. brachyandra* may well become endangered, as swampy, moist areas are frequently drained for agriculture, building, etc.

Vouchers: *Compton 16359* (NBG); *Salter 8718* (NBG), *9046* (BOL).

4. **Wachendorfia parviflora** *W.F. Barker* in Journal of South African Botany 15: 39 (1949); W.F. Barker: 207 (1950). Type: Cape Peninsula, Camps Bay, *Salter 7457* (NBG, holo.!).

Rhizomatous perennial herb, 0.1–0.4 m tall, usually dwarf, 0.1–0.2 m. *Rhizome* small globose-ovoid, oblong, 5–25 mm in diameter. *Leaves* annual, erect or spreading, linear to lanceolate, usually falcate and longer than inflorescence, blue-green, softly hairy, up to 360 × 25 mm. *Leaf anatomy*: palisade layer one cell thick; cuticle with intermediate lignification; sclerenchyma caps well developed; subsidiary cells rectangular; mucilage canals small. *Culm* short (usually less than 0.2 m); culm, peduncles and pedicels covered in short glandular hairs. *Inflorescence* a very short, dense panicle; peduncles very short, densely clustered on axis. *Bracts* herbaceous, green, erect, often produced beyond the flowers. *Tepals* dull yellow, fading brownish purple, segments narrow, 15–25 × 3–6 mm, upper segments usually broader than the rest, lowermost tepal isolated. *Stamens*: two thirds length of tepals, 10–12 mm long; anthers 1.5–2.0 × 0.5 mm. *Style*: two-thirds length of tepals, 11 mm long. *Fruit* a dry capsule, broader than long, 6–7 × 11–14 mm; carpels obtuse, covered in glandular hairs. *Seeds* globose, coarsely hairy, 2–4 mm in diameter. Figure 6.

Flowering time: early August to late September, with a peak in early September.

Distinguishing features: dwarf habit; erect herbaceous bracts; tepals very narrow.

Distribution and habitat: *W. parviflora* is essentially a species of the western Cape, ranging from Nieuwoudtville to the Cape Peninsula and McGregor (Figure 7). There is a record from near Soebatsfontein and another from 15 km east of Hondeklipbaai (3017BB), which suggests that this species probably occurs all the way up the west coast as least as far north as Hondeklipbaai. This area is under-collected (Gibbs Russell *et al.* 1984) and it may be more common and widespread in the area.

W. parviflora grows on both sandstone and granite derived soils, and there are a few records from shale areas. The species is found at altitudes ranging from 15–±500 m a.s.l. in habitats ranging from dry, sandy hollows in coastal fynbos to moist, rocky ledges in thick mountain fynbos. It is often found in association with *W. paniculata*.

Status: uncertain, probably uncommon and sparse throughout its range. Appears to be replaced by *W. paniculata* in many apparently suitable areas.

Vouchers: *W.F. Barker 4600* (NBG), *W.F. Barker 9-8-1935* (BOL); *Hanekom 1168* (PRE); *Johnson 236* (NBG); *Salter 7457* (NBG).

DETAILED MORPHOLOGICAL OBSERVATIONS

Rhizome

Wachendorfia possesses a distinctive rhizome, containing a red fluid rich in arylphenalenone pigments. The air-dried rhizome varies in diameter from 5–50 mm, although the fresh rhizomes may be twice this size. The shape is usually spherical to ovoid, although irregular shapes may occur. An air-dried rhizome is usually covered by a papery tunic composed of the dry leaf bases.

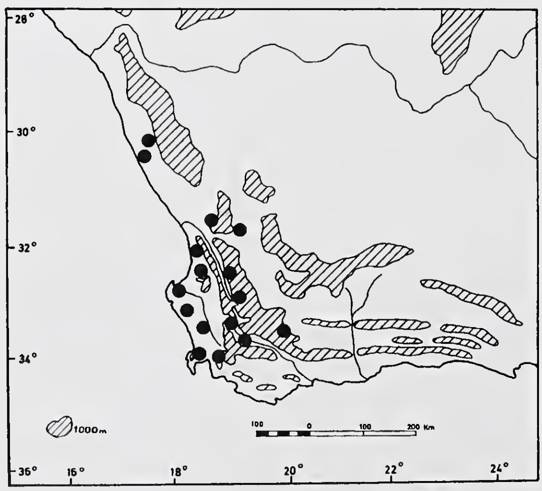

FIGURE 7.—Distribution of *W. parviflora*.

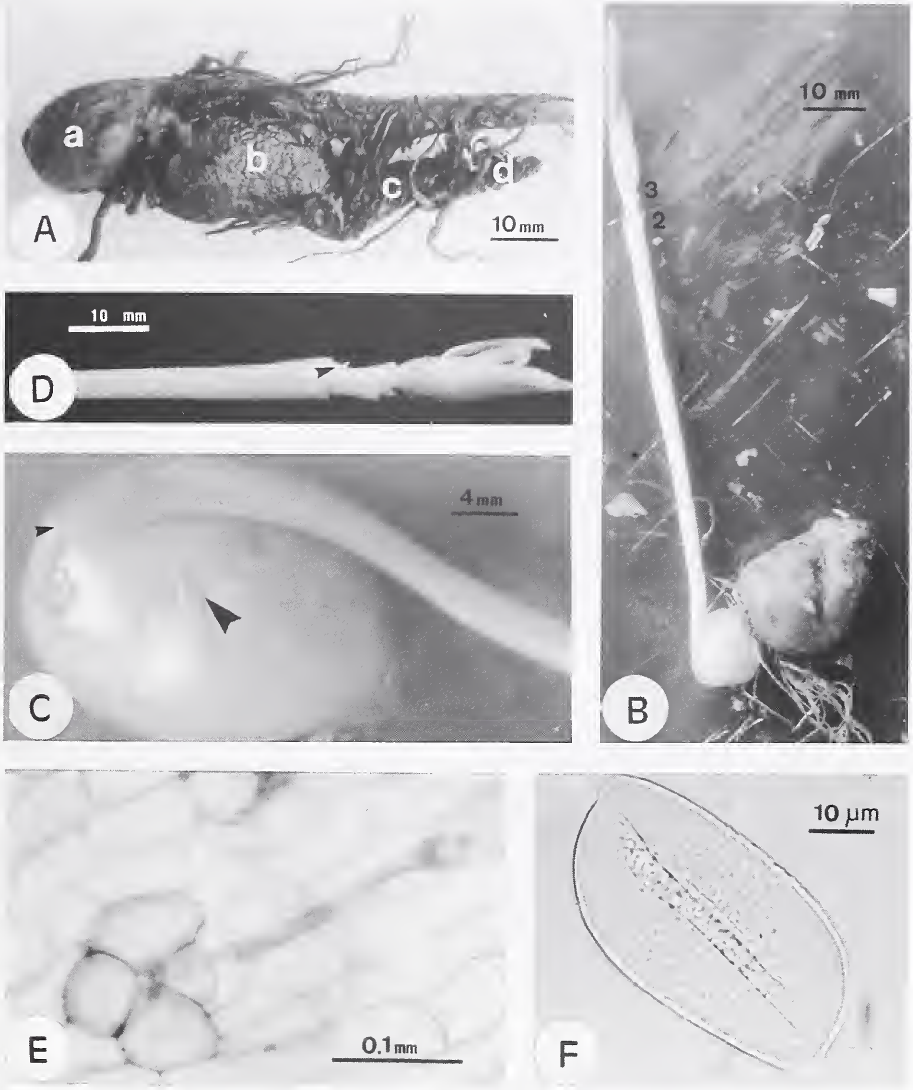

FIGURE 8.—A, *W. paniculata*: rhizome morphology, showing the three previous years' shrivelled rhizomes, separated in each case by a cluster of adventitious roots. a, active rhizome; d, three year old rhizome. B, *W. parviflora*: rhizome and culm with leaves removed. Culm nodes 1 and 2 with amplexicaul leaves; node 3 and onwards with spiral arrangement of leaves; nodes 2 and 3 with small sterile buds visible. C, *W. paniculata*: rhizome with all rhizome leaves removed; large node ringing middle of rhizome is node 2, axillary bud visible (large arrow); node 3 visible near base of culm (small arrow). D, E, *W. parviflora*: D, close up of young culm, nodes 2 & 3 visible, the sterile bud of node 2 arrowed; E, pileate epidermal hair, note four enlarged basal cells and multicellular hair construction. F, *W. paniculata*: light photomicrograph of pollen grain, illustrating central sulcus, proximal verrucae and micropore-pitted border.

A new rhizome is produced every year, with the previous year's rhizome remaining attached to the present year's rhizome. The old rhizome shrivels, until all that remains is the extensive system of vascular traces. Occasionally up to three old rhizomes may be found attached in sequence to the current rhizome. A cluster of thin, short adventitious roots sprouts from between each rhizome (Figure 8A, B).

Each rhizome has three nodes, each with a 'rhizome leaf' and an axillary bud (Figure 8C). The axillary buds are arranged distichously. Each axillary bud is capable of producing a new rhizome, although only one is actually produced. The new rhizome may be produced below or to the side of the parent rhizome. This means that next year's rhizome will be exploring new soil, either deeper or some horizontal distance from the parent. This may be an important function given the absence of tap roots. The annual flowering shoot is formed by the apical bud, resulting in a sympodial growth form. *W. thyrsiflora* may produce stoloniferous lateral outgrowths from the main rhizome, some of which may ultimately extend several metres. These extended rhizomes are then capable of producing new ramets. Vegetative reproduction is common in monocots, and seems to be an important feature of *Wachendorfia*.

The rhizomes stain positive for starch. In *W. paniculata* and *W. parviflora* the amyloplasts are concentrated

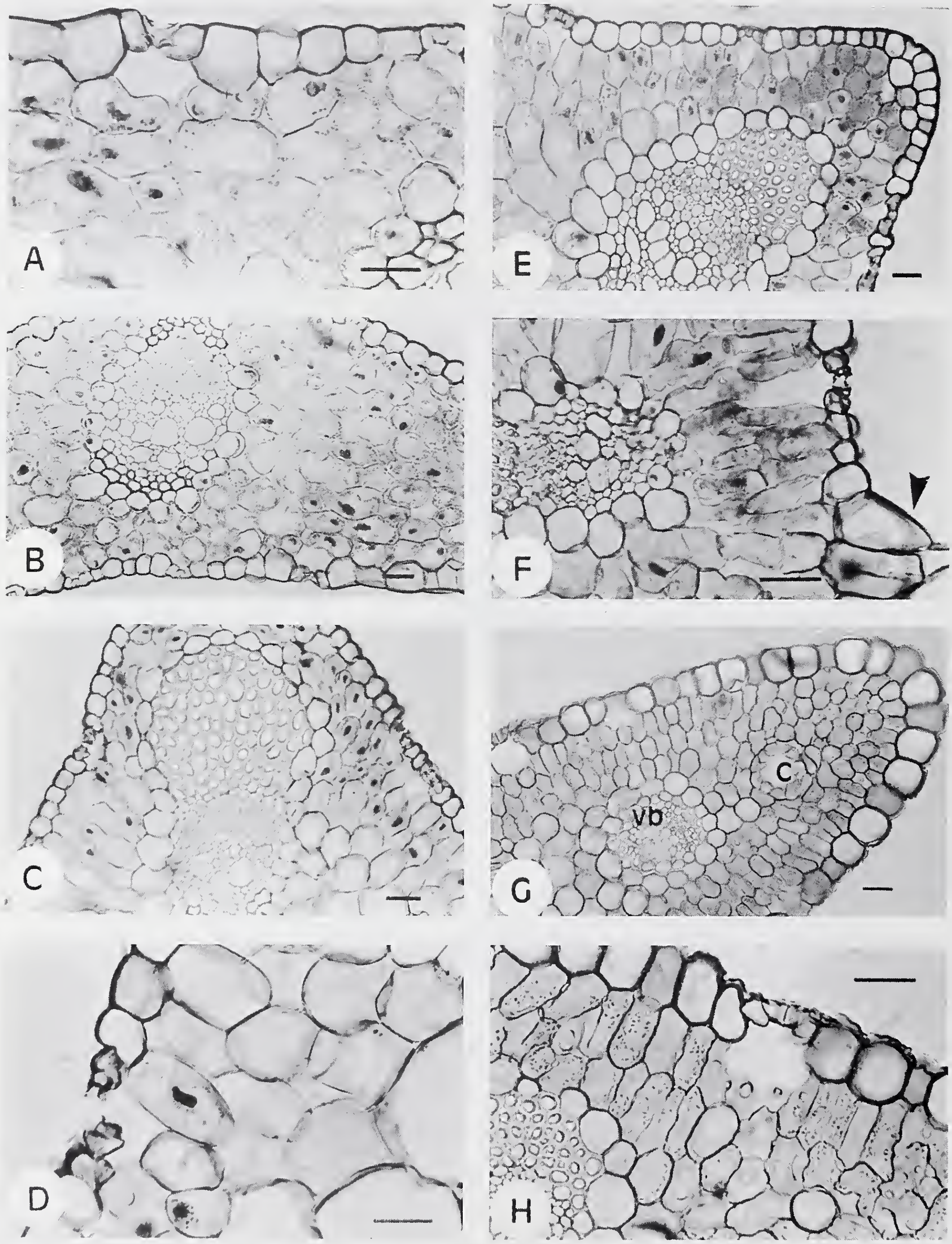

FIGURE 9.—Leaf anatomy of *Wachendorfia*; scale bar, 250 µm. A, B, *W. thyrsiflora*: A, leaf section illustrating kidney-shaped subsidiary cells and poorly defined palisade layer; B, vascular bundle with small sclerenchyma caps. C, D, *W. paniculata*: C, vascular bundle with large sclerenchyma caps; D, stoma with twin epidermal lips and single palisade layer. E, *W. brachyandra*: variable palisade width and bundle with large cap. F, *W. parviflora*: single palisade layer and trichome base with four swollen epidermal cells (arrowed). G, *Dilatris pillansii*: leaf edge with double palisade layer: c, mucilage canal; vb, horizontally aligned vascular bundle; spaces between densely packed cortical cells are the result of lobing. H, *D. pillansii*: stoma with twin epidermal lips and kidney-shaped subsidiary cells.

within the vascular stele, with almost none in the cortex. In *W. thyrsiflora* amyloplasts are equally common in the cortex and the stele. The reasons for this variation are unknown, but may be related to the persistence of the rhizome of *W. thyrsiflora*, resulting in an extremely long underground organ.

The xylem elements have an amphivasal arrangement, which is similar to that reported for the Restionaceae by Linder (1990).

Leaf morphology

Although the plicate leaves of *Wachendorfia* are distinctive, they often show considerable intraspecific variation. The colour varies from dark green through to light yellow-green, and is often a function of leaf age. The shape may vary within a species, some populations of *W. paniculata* having almost needle-like leaves, and others having broad, falcate leaves. *W. thyrsiflora* usually has large ensiform leaves, whereas *W. brachyandra* has lanceolate or falcate leaves. *W. parviflora* is normally characterised by falcate leaves, but may frequently have lanceolate leaves. *W. thyrsiflora* has distinctly longer and broader leaves than any of the other species (up to 900 × 80 mm). The other three species show much interplant variation in leaf size, but are all within approximately the same range, up to 400 × 40 mm. There seems to be some altitudinal variation in leaf size and shape in *W. paniculata*, with specimens growing at high altitudes tending to have extremely long, narrow, linear leaves.

Wachendorfia leaves originate from both the rhizome and the culm. There are usually three large rhizome leaves, arising from the three rhizome nodes (Figure 8C). These leaves sheath the culm at the base. The culm leaves fall into two types: the lowest two are amplexicaul and opposite, whereas those further up the stem are spirally arranged (Figure 8D). The lower leaves thus give the distinct impression of being two-ranked. The leaves are always firm in texture, longitudinally plicate and entire. The leaves of *W. thyrsiflora* and *W. brachyandra* are always glabrous or very nearly so, while those of *W. parviflora* are distinct in having a dense coating of numerous short hairs (Figure 8E). *W. paniculata* leaves vary from being nearly glabrous to densely hairy with long white hairs. Within-plant variation in leaf hairiness is small, although within-population variation may be great in this species. There is no obvious ecological reason for the difference in leaf hairiness within the species, as it does not seem to follow a gradient of rainfall, altitude or any other single factor.

The dense leaf hairs in *W. parviflora* are of two types. Pointed, unicellular hairs are by far the most common, outnumbering the pileate, tricellular hairs by about 5:1. Adaxial and abaxial leaf surfaces are equally hairy. Four or occasionally five large epidermal cells support the base of each hair. The unicellular hairs taper to a point and appear to have hollow bases, whereas the tricellular hairs have small terminal cap cells that may be glandular (Figure 8E).

The two species confined to permanently damp habitats (*W. thyrsiflora* and *W. brachyandra*) have glabrous leaves, whereas the two dryland species (*W. paniculata* and *W. parviflora*) usually have hairy leaves.

Leaf anatomy

The leaf anatomy of *Dilatris pillansii* W.F. Barker, *D. corymbosa* Berg., and the four species of *Wachendorfia*, was examined. *Wachendorfia* leaves are plicate, and both thinner and wider than the narrow, rigid leaves of *Dilatris*, which have a number of special associated features.

The palisade layer in *Dilatris* is two cells wide (Figure 9H), which is a similar arrangement to the twin layer of columnar palisade cells in *Conostylis* R. Br. (Green 1959). *Lachnanthes* Ell. lacks a palisade layer altogether (Simpson & Dickison 1981). There is thus a range of palisade structures within the family. The Cape genera reflect this variation well, with *Dilatris* having a two cell layer, *W. thyrsiflora* without a distinct layer (Figure 9A), and the other *Wachendorfia* species with either a one or a two cell layer (Figures 9C−F). Cortical air spaces are absent in *Dilatris* and the cortical cells are lobed (Figure 9H). All *Wachendorfia* species have air spaces between the isodiametric cortical cells (Figures 9A−F).

The epidermal cuticle is thick in *Dilatris, W. thyrsiflora* and *W. paniculata*, but is noticeably thinner in *W. parviflora* and *W. brachyandra*. Lignification of the epidermal layer is light in all taxa bar *W. parviflora*, in which extensive lignification is evident (Figure 9A−H).

Stomata in *Dilatris* and *Wachendorfia* species are paracytic. The epidermal lip has a well-developed upper component and a lower lip of about half the length of the upper. This double epidermal lip is also recorded in *Lachnanthes* (Simpson & Dickison 1981). Green (1959) made no mention of these epidermal lips in his study of the Australian genus *Conostylis*, although his drawings show slight spurs on the outer edges of the stomata. *Dilatris* has a kidney-shaped subsidiary cell (Figure 9H), a feature which it shares with *W. thyrsiflora*. All other *Wachendorfia* species have rectangular subsidiary cells. Stomata appear to be equally common on both sides of the leaf and are very slightly sunken relative to the epidermal layer. Large substomatal cavities are present in all taxa.

In *Wachendorfia*, the large first order vascular bundle within the extreme edge of the leaf closest to the culm, lies horizontally (i.e. tangential to the culm axis), whereas all others in the leaf are vertically orientated (i.e. radial to the culm axis). This feature is also found in *Conostylis* (Green 1959). This may be the result of the leaf sheathing around the rhizome and the culm, thus flattening one edge of the leaf and distorting the apparent bundle position. Sclerenchyma cap development in the vascular bundles is very variable. *W. thyrsiflora* has poorly developed caps, whereas in *Dilatris* and *W. parviflora* they are well-developed. This feature is variable in both *W. brachyandra* and *W. paniculata*, and in the latter the bundles may be exceptionally well developed.

W. thyrsiflora has larger leaf cortex mucilage canals than the other species in the genus. This may be an allometric feature associated with the overall large size of the species or the result of ecological or phylogenetic factors. We suggest that it does have ecological relevance, as the various species' leaf sections were taken from leaves of the same size (thus reducing any allometric effects), and *W. thyrsiflora* is unique in being confined to permanently damp sites. Large quantities of mucilage can be seen in cut sections of *W. thyrsiflora* leaves and most of this appears to come from the large canals in the leaf. *Dilatris* has a single large canal within the leaf (Figure 9G), and this is always located in the side of the leaf closest to the aerial stem. There are a number of other smaller canals scattered throughout the leaf cortex which may act as mucilage ducts.

Floral morphology

Considerable interplant and interpopulation variation occurs in the length of the inflorescence, the number of cymes produced, the number of flowers in a cyme, the size and colour of the flowers, the degree of perianth spreading, and the size of the nectaries.

Wachendorfia flowers are enantiomorphic. The style of some flowers is sharply directed to the right, whereas in other plants it is deflected to the left (Figure 2). In both cases, one of the three stamens is borne close to the style, the other two are deflected in the opposite direction. *Dilatris* is also enantiomorphic, but differs in that both left- and right-handed flowers may be found on the same inflorescence.

The upper three tepals in *Wachendorfia* have pale markings surrounded by dark rings which may act as nectar guides. There is much interplant variation in the contrast, size, and shape of these markings. Large 'semi-extrafloral' nectaries are formed by the bases of the outer upper and the two adjacent inner tepals, one being present on each side of the flower. These are elongated into spurlike structures clearly visible on the outside edges of the flowers. Significant quantities of nectar are produced, which may persist even after the flower itself has withered. Nectar is also produced long before the flower is open. Sugar concentration in an open flower is about 20%, rising to 50% in a withered flower (Ornduff & Dulberger 1978).

The genus is essentially spring flowering, although there are some intra- and interspecific differences worth noting. High altitude forms of *W. paniculata* are noted for their late flowering. The species has an extremely long flowering period, and this may be attributed to the varied habitats in which the species is found. *W. thyrsiflora* is often found flowering in late summer. This might be a reflection of its moist habitat, as severe moisture stress is unlikely, perhaps allowing this species to flower much later than the other species which favour drier habitats. *W. parviflora* is interesting in that it flowers early, with no flowering recorded later than September. It is often the only species of the genus in flower in early August.

The three dryland species can be separated on flower structure. In Figure 10 three floral measurements are plotted for *W. parviflora*, *W. brachyandra*, and *W. paniculata*. On the y-axis a ratio of stamen (= style) length over maximum tepal length for each flower is plotted, (demonstrating the distinctness of *W. brachyandra*), and on the x-axis the maximum tepal width recorded for each flower is given (demonstrating the distinctness of *W. parviflora*). *W. thyrsiflora* is a very distinct species in many different ways (habitat, size, anatomy), and for this reason is not included in this analysis. The figure illustrates how the three species can be separated by a combination of floral characters, but it should be noted that it does not demonstrate the existence of clearcut phenetic groups.

Pollen

Erdtman (1966) recognized three pollen types within the Haemodoraceae. Six genera, including both *Dilatris* and *Wachendorfia*, are characterized by monosulcate pollen (20–90 μm long) with a 'usually not very distinct' exine stratification and sexine pattern. *Barberetta* was not studied by Erdtman (1966). Simpson (1983) published a systematic palynological survey of the Haemodoraceae, in which the pollen was investigated by light microscopy, and both scanning and transmission electron microscopy, thus allowing a detailed characterisation of the wall structure. He included two species of *Dilatris*, *Wachendorfia thyrsiflora* and *Barberetta* in his study, and his observations provide a useful descriptive base for the present study which included the other three species of *Wachendorfia*.

Dilatris pillansii and *D. corymbosa* possess very similar pollen grains, are monosulcate and heteropolar, with verrucate to baculate non-apertural sculpturing and gemmate to psilate apertural sculpturing (Figure 11A). Grains are approximately 50 μm long (polar) and 25 μm wide (equatorial). The exine surface appears to be quite

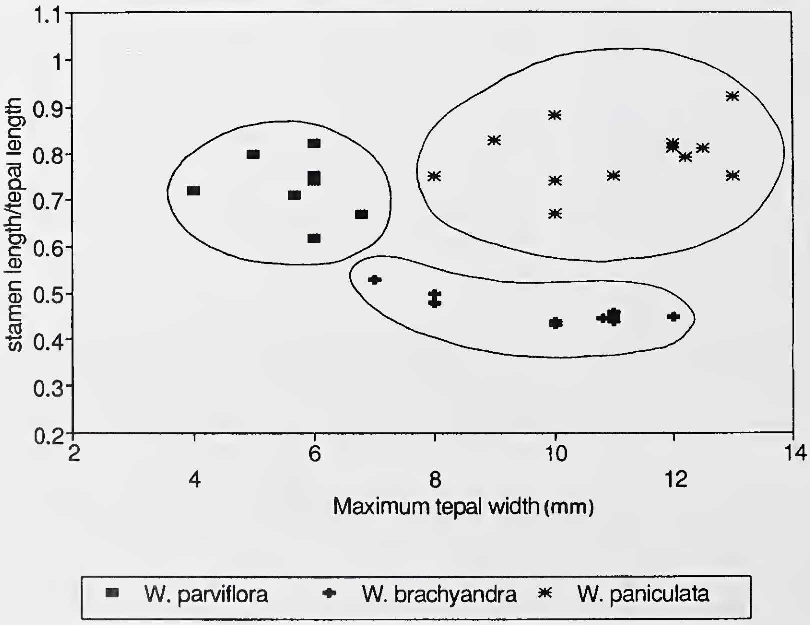

FIGURE 10.—Scatter diagram of the maximum tepal width against the ratio of stamen/petal length for *W. parviflora*, *W. brachyandra* and *W. paniculata*, showing how these species can be separated morphologically.

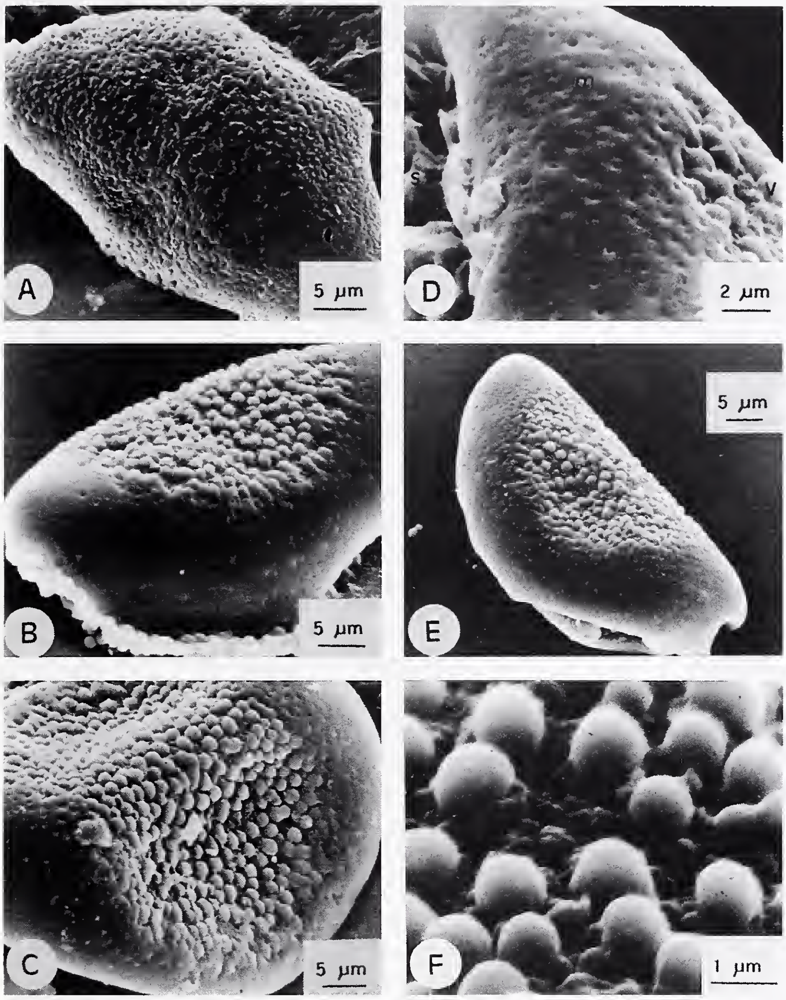

FIGURE 11.—Scanning electron micrographs of pollen grains. A, *Dilatris corymbosa*: reticulate exine. B, *W. thyrsiflora*: broad micropore-pitted border. C, *W. parviflora*: verrucae patterning. D, *W. brachyandra*: v, verrucae; m, micropore-pitted border; s, sulcus. E, F, *W. paniculata*: E, heteropolar, boat-shaped grain; F, close-up of verrucae and granular secondary exine sculpturing beneath.

different from the exine of *Wachendorfia* pollen, as the verrucae seem to have coalesced to form a more continuous bumpy pattern. *Dilatris* also has a far less obvious micropore-pitted aperture border.

Wachendorfia pollen is monosulcate and heteropolar, with a convex aperture wall consisting of widely separated, two-layered baculate exine elements, over a relatively thick two-layered, fibrillar intine (Simpson 1983). The concave non-apertural wall is proximally verrucate, with a granular appearance between the verrucae (Figure 11F). The verrucae thus appear to 'saddle' the pollen grain (Figures 8F; 11B–F). The aperture wall is encircled by a smooth border pitted with micropores (Figure 11B–F). The 'coarsely granular, distinctly convex operculum' noted by Erdtman (1966) is an aperture wall with an outer layer of closely spaced exine structural elements, a point noted by Simpson (1983). These apertures often disintegrate during acetolysis, probably because of the lack of continuous exine material between the elements. The grains are distinctly hemispheric in shape. All species have grains 40–50 × 20–25 μm. In all species the size of the exine verrucae is relatively constant, about 1 μm in diameter, and all species have the granular substance visible between the verrucae. This granular layer is the lower layer of the two-layer exine. *W. thyrsiflora* (Figure 11B) differs from the rest of the genus in that the distance between the sulcus and the start of the verrucae, i.e. the width of the micropore-pitted border, is twice as great as in the other species. There is thus no reliable way to identify *Wachendorfia* pollen, with the exception of that of *W. thyrsiflora*, to species level.

The pollen of *Barberetta* is virtually identical to that of *Wachendorfia*. This suggests that *Barberetta* is more closely related to *Wachendorfia* than it is to *Dilatris*.

Seeds

The seeds of *Wachendorfia* are all ovoid or spherical, about 2 mm in diameter, and covered in numerous short hairs (Figure 12B–F). There is little interspecific variation, and they cannot be reliably used for species identification. Hair length and width shows very little variation. All the species have curious verrucae on the hairs (Figure 12E, F), and their function and origin is not known.

W. thyrsiflora has the most distinctive seed, as they are large and somewhat kidney-shaped. When viewed in a

SEM, the hairs on the seed also have a greater density of verrucae than the hairs of other species. The seed dispersal biology is unknown, with hydrochory and anemochory possible. The seed of *W. thyrsiflora* has been observed floating on streams (pers. obs.), and as this species is generally associated with streams, hydrochory may be important here.

Pollination biology

The few studies on the evolutionary significance of enantiomorphy have suggested that it is probably a feature which promotes outcrossing, that is, increases the level of intermorph pollination (Wilson 1887; Ornduff & Dulberger 1978). This conclusion is based on the findings that *W. paniculata* has a weakly developed self-incompatibility system, and that intermorph crosses produce more seeds than self-pollinations or intramorph pollinations. Selection for outcrossing cannot be the driving force behind the evolution of the *Dilatris* flower structure, as left- and right-handed flowers are found on the same plant. The

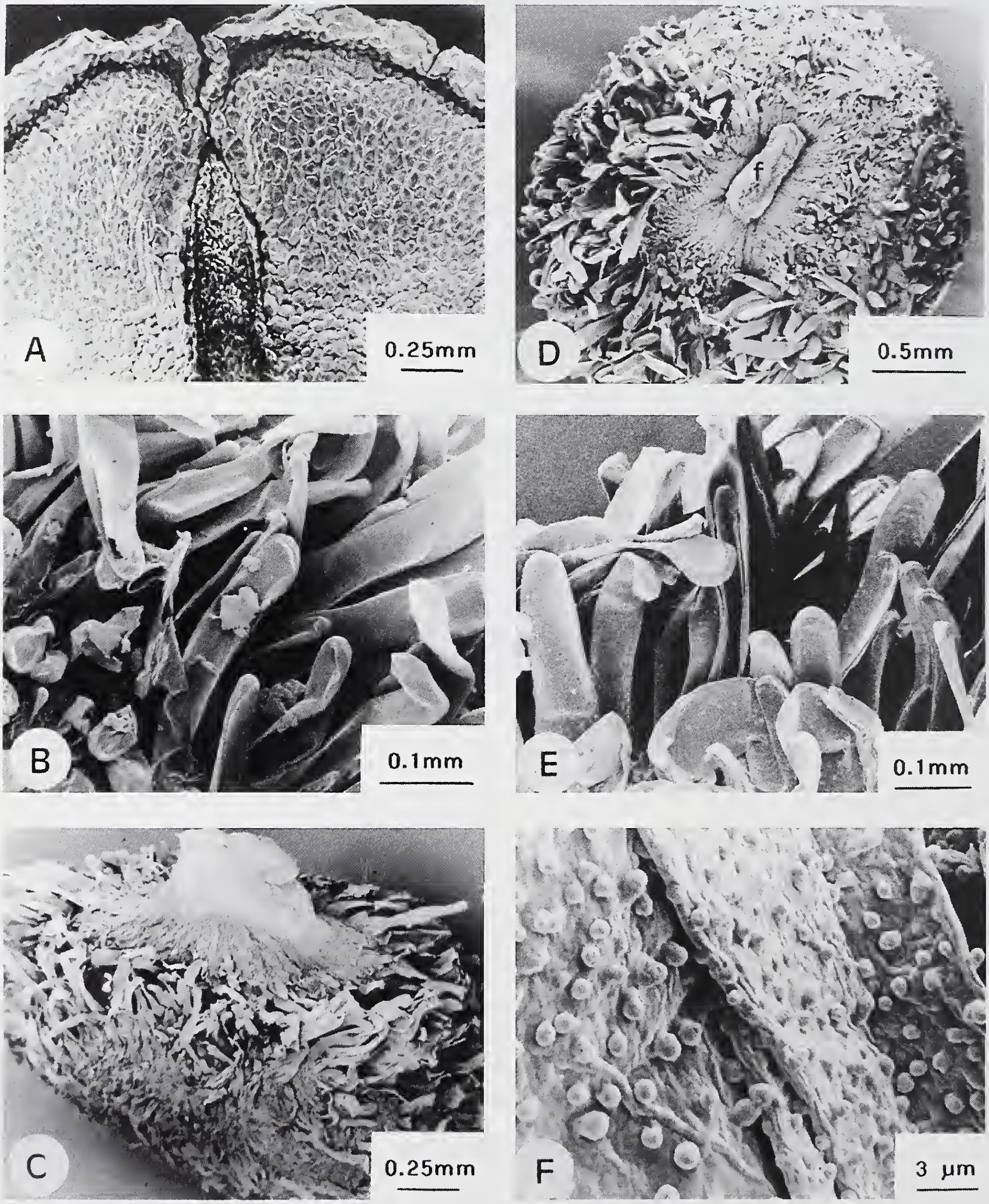

FIGURE 12.—Scanning electron micrographs of seed. A, *Dilatris viscosa* L.f.: disc-like seed with a central funicle and reticulate patterning. B, *W. brachyandra*: seed hairs often have relatively few verrucae. C, *W. paniculata*: typical raised funicle and hairy, oval seed. D, *W. brachyandra*: spherical seed with the usual central funicle(f). E, *W. parviflora*: seed hairs and verrucae. F, *W. thyrsiflora*: dense verrucae on its seed hairs.

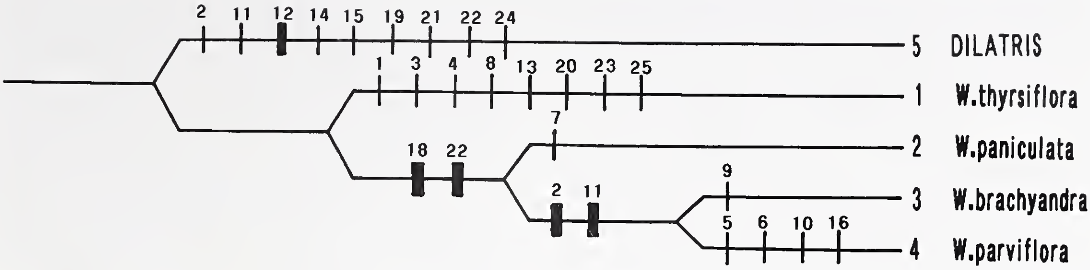

FIGURE 13.—Cladogram for the species in *Wachendorfia*. All characters are indicated; those that are phylogenetically informative are indicated by thicker lines. The length of the components indicates the patristic distances on the diagram. Character codes are given in Table 1, and the distribution of the characters in Table 2.

evolutionary history behind such a strange system is completely unknown (Ornduff & Dulberger 1978).

The seemingly wasteful production of large quantities of 'extrafloral' nectar, often prior to anthesis, is once again difficult to explain in evolutionary terms, and deserves further study. The nectaries open to the outside of the flower and nectar stealing is therefore very easy, as the 'thief' does not have to get anywhere near the pollen or stigmatic surfaces. Ants are seldom seen on the plants due to the glandular hairs on the stem, so the 'extrafloral' nectar does not appear to have any function in feeding 'ant guards' (see Faegri & Van der Pijl 1966).

The pollinators are unknown. This would be a rewarding field of study, as the unusual floral morphology may reflect interesting evolutionary/ecological interactions. One of the problems with the pollination syndrome is that in all species, except *W. brachyandra*, the stigma and anthers seem too far apart for most insects to touch when visiting the flower. We might predict that seed set would be greater in *W. brachyandra* than in the other species (ease of pollination), but preliminary observations do not support this prediction. There must therefore be some insects which can pollinate the other species. These insects would have to be significantly larger than the common honeybee, *Apis mellifera*, as this species is not able to reach the anthers. The carpenter bee, *Xylocopa caffra*, is large enough but it is very seldom seen on low growing *Wachendorfia*, as it tends to favour tall shrubs and small trees, e.g. *Virgilia oroboides*. The first author has seen tabanid flies (family Tabanidae) taking nectar from *W. parviflora* and *W. paniculata*, and in the process, the wings of this large-bodied fly touched the anthers. It is possible that this group of flies may be important pollinators of the genus due to their size and anthophilous behaviour, but more observations are needed. Other potential pollinators include numerous small beetles that appear to feed on the pollen. These beetles clamber over the anthers and may effect a degree of 'mess and soil' pollination.

Phylogeny and speciation

The most parsimonious cladogram is given in Figure 13. The patristic distances (i.e. the degree of divergence from its ancestor) of each component is indicated by the relative length of that component. All the characters, including the autapomorphies, have been indicated on the diagram. Phylogenetically informative characters are indicated by thicker lines.

W. thyrsiflora is basal in the genus and has many more autapomorphies than any of the other species, indicated by the long patristic distance from its basal node. This suggests that *W. thyrsiflora* has diverged morphologically from the rest of the genus. It also occupies the most peculiar habitat, in perennially wet marshes and along streams, whereas the other species are all in habitats that are at least seasonally dry, and the morphological divergence may reflect this habitat specialisation.

The remaining three species occupy relatively similar habitats, and also show relatively low patristic differences between them. *W. paniculata* has a wide ecological and geographical range, but is restricted to well-drained habitats. *W. brachyandra* is restricted to the southwestern Cape, where it occurs in seasonally wet places and forest margins. There is no evidence to date of it occurring with any of the other species, but the stamen-petal ratio may reflect a pollination isolation mechanism.

W. parviflora is often found occurring with *W. paniculata* and appears to be ecologically very similar. However, there is a temporal separation in the flowering time, with *W. parviflora* flowering earlier than *W. paniculata*. This suggests that *W. parviflora* may be a neotenous form of *W. paniculata*. Morphologically, the hairy leaves and narrow tepals may be juvenile structures (although this has not been substantiated with ontogenetic studies on *W. paniculata* and *W. brachyandra*). The speciation mechanism that may lead to such a neotenous form is obscure. Unfortunately this species has not been investigated cytologically, so the possibility of cytological reorganization underlying this evolution is not excluded.

The short patristic distance between the ancestral node and *W. paniculata* suggests that the ancestral habitat of *Wachendorfia* was well-drained. Conversely, the large patristic distance to *W. thyrsiflora* suggests that its perennially wet habitat is a derived habitat. It is interesting that the diversification in the genus occurred in the dryland clade, rather than the marshland clade. Although the total patristic distances of the *W. thyrsiflora* clade and the *W. paniculata* clade are the same, the *W. paniculata* clade, because it contains three species, has a much wider range of variation. This is expressed morphologically by the different taxa showing different patristic values, phenologically by the much wider range of flowering times and ecologically by the range of substrates and moisture regimes. The total geographical ranges of the two clades are the same. These results would caution against automatically assuming that because the wetland taxon is taxonomically isolated, it represents the ancestral habitat.

CONCLUSIONS

Wachendorfia consists of three well-defined species and a fourth extremely variable species. This latter species, *W. paniculata*, has been the cause of much confusion in the past: at least seven specific names were given to the various forms. This variation is continuous, making the recognition of intraspecific taxa totally arbitrary. There is never any real geographic separation of these forms, so the use of subspecific or varietal rank would be inappropriate (Stuessy 1990). However, there is a form that shows a type of geographical separation along with a distinctively lax morphology (*W. paniculata* form 2). Although this form is confined to the mountains between Ceres and Pakhuis Pass, it is not the only form in the area, so subspecific rank would not be appropriate (no allopatry).

Linder (1990) found that 'using only macro-morphological structures at specific level in the Restionaceae only reflects a portion of the available information and reliance on such a small portion of the available data set may lead to mistakes when assessing the relationships among species'. The present study supports this view and we feel that the reliance on macro-morphological features is often the reason for inadequate, confusing species delimitations within *Wachendorfia*. The present study assessed not only macro-morphological variation within *Wachendorfia*, but also pollen and seed coat features, rhizome storage products, and basic features of leaf anatomy. It is hoped that this broader data base strengthens the proposed classification of *Wachendorfia*.

The cladistic analysis suffered from a lack of informative characters and the resulting cladogram should be interpreted with caution. However, the diagram of patristic distances (Figure 11) illustrates the difference between the habitat specialist (*W. thyrsiflora*) and the habitat generalists, the former having many more derived traits, suggesting that ecological specialization has occurred. *W. parviflora* is notable for the number of derived characters that support the idea of it being a neotenous species.

The reproductive biology is not sufficiently well known to understand the evolution of the peculiar form of floral enantiomorphy in *Wachendorfia*. Although there is a phylogeny at generic level (Simpson 1990) the functional purpose of enantiomorphy and extrafloral nectaries is not understood. This may well be linked closely to the pollination biology in the genus.

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An overview of *Penicillium* (Hyphomycetes) and associated teleomorphs in southern Africa

A.L. SCHUTTE*

Keywords: *Eupenicillium*, fungi, Hyphomycetes, *Penicillium*, overview, southern Africa, *Talaromyces*, taxonomy

ABSTRACT

Literature on the hyphomycete genus *Penicillium* Link and its teleomorphs, *Eupenicillium* Ludwig and *Talaromyces* C.R. Benjamin, is surveyed in the Republic of South Africa, Lesotho, Mozambique, Namibia, Swaziland and Transkei up to 1990. References are grouped under the headings, general mycology, plant pathology, industrial application, medical importance, mycotoxins and chemical work. An alphabetical list of the species recorded in southern Africa as well as the host and/or substrate from which each species has been reported is presented with relevant literature references; specimens in various culture collections are also incorporated. Although most of the known *Penicillium* species have already been reported from southern Africa, in-depth work is still required in all fields of research concerning this genus.

UITTREKSEL

Literatuur aangaande die hifomiseetgenus *Penicillium* Link en sy teleomorwe *Eupenicillium* Ludwig en *Talaromyces* C.R. Benjamin in die Republiek van Suid-Afrika, Lesotho, Mosambiek, Namibië, Swaziland en Transkei is nagegaan tot 1990. Die verwysings word gegroepeer onder die opskrifte mikologie, plantpatologie, industriële toepassing, mediese belang, mikotoksiene en chemiese werk. 'n Alfabetiese lys van die spesies wat in suidelike Afrika aangeteken is, asook die gasheer en/of substraat waarop elke spesie aangemeld is, word met die toepaslike verwysings gegee; eksemplare in verskeie fungus-versamelings word ook ingesluit. Alhoewel die meeste van die bekende *Penicillium*-spesies reeds in suidelike Afrika aangeteken is, is diepgaande werk op alle navorsingsgebiede rondom hierdie genus steeds nodig.

INTRODUCTION

'Species of *Penicillium* are so abundant and so conspicuous in all sorts of stale or decaying organic matter that they constitute a part of the common conception of mould, and are loosely referred to as 'blue' or 'green' mould' (Raper & Thom 1949). Representatives of this multi-faceted genus are of ecological importance because they are abundant and widespread in the environment; they are fruit deteriorators and contribute greatly to post-harvest decay; they have industrial applications such as in cheese-making; and they produce secondary metabolites and mycotoxins, including the indispensable antibiotics.

The generic name *Penicillium* (Latin, *penicillus* = little brush) was first introduced in 1809 by Link who very briefly described the genus with three species, namely *P. candidum* Link, *P. expansum* Link and *P. glaucum* Link. The true identity of these fungi has been difficult to determine, but an apple-rotting fungus was linked to *P. expansum* by Thom (1910). Although the validity of the generic name has been questioned over the years, Hawksworth (1985) concluded that *Penicillium* Link should be considered correct and indicated that he had previously designated a neotype of *P. expansum* Link as the type species of the genus.

Succeeding the works of Thom (1910, 1930), the manual by Raper & Thom (1949) has been the standard work on *Penicillium* for nearly 30 years. Subsequently, a new era in *Penicillium* identification was heralded by Pitt (1973), who used the ability of isolates to grow at reduced water activity, correlated with penicillus types, as well as growth rates at 5°C and 37°C, as differential criteria. This concept was later fully developed in a monograph (Pitt 1979). Shortly afterwards, a well-illustrated atlas of penicillia by Ramirez (1982) was published. However, the value of Pitt's (1979) guide to the taxonomy of *Penicillium* was confirmed at the First international *Penicillium* and *Aspergillus* workshop (Samson & Pitt 1985), when Pitt's species concept and methods were incorporated in the recommendations for future taxonomic practice in this genus.

Previously, the name *Penicillium* was applied to both the hyphomycetous and ascomycetous states. However, separation of the teleomorphic states of *Penicillium* from the anamorph, as implemented by Pitt (1979), is in accordance with Art. 59 of the International Code of Botanical Nomenclature and is of practical value for the taxonomist. Stolk & Scott (1967) re-introduced the use of the teleomorph name *Eupenicillium* Ludwig for a portion of the genus *Penicillium*. Monographic contributions to the genus *Eupenicillium* were made by Scott (1968a, b) and Stolk & Samson (1983). The teleomorphic genus *Talaromyces* C.R. Benjamin is separated from *Eupenicillium* on the basis of ascocarp morphology. The former genus is characterised by the production of gymnothecia composed of loosely intertwined hyphae, as opposed to cleistothecia. Stolk & Samson (1972) as well as Pitt (1979) have contributed to the taxonomy of this group.

A multidisciplinary approach to the identification of *Penicillium* is becoming more prevalent (Bridge *et al.* 1985). Protein electrophoresis (Bent 1967), the API ZYM testing system (Bridge & Hawksworth 1984), pyrolysis gas chromatography (Söderström & Frisvad 1984), physiological and biochemical methods (Bridge 1985), enzyme electrophoresis (Cruickshank & Pitt 1987), studies on

* Mycology Unit, Plant Protection Research Institute, Private Bag X134, Pretoria 0001.
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thermal denaturation of DNA (Paterson *et al.* 1990), electron microscopy (Ramirez 1982; Kozakiewicz 1989) and the production of secondary metabolites and mycotoxins (Frisvad & Filtenborg 1983; Frisvad *et al.* 1990) have recently been used to supplement traditional methods of identification.

Members of this genus identified at the Mycology Unit in recent years were often found to differ somewhat from the descriptions given by Pitt (1979). This raised the question of whether these variations are consistent for all South African isolates. In addition, preliminary investigations indicated that *Penicillium* species are frequently only briefly mentioned in publications or included in lists of fungi from surveys. It was therefore considered advantageous to gather this scattered information in order to compile a list of *Penicillium* species recorded in southern Africa, to bring this information in line with modern taxonomic systems, and to indicate areas requiring further research.

This paper is an overview of publications dealing with all aspects of the *Penicillium* species reported in South Africa, Lesotho, Mozambique, Namibia, Swaziland and Transkei up to 1990. Literature is grouped according to various fields of research and presented in chronological order. The National Collection of Fungi, including the dried collection and the culture collection, collections donated to the Mycology Unit, the collection of the Medical Research Council as well as catalogues of international culture collections, served as additional sources of information. Foreign isolates used for chemical work, have been mentioned but not listed. No attempt has been made to verify published data, the identity of *Penicillium* isolates, or any other information.

OVERVIEW OF LITERATURE

General mycology

The first published record of the genus *Penicillium* in southern Africa appears to be that of *P. digitatum* (Pers. ex Fr.) Sacc. on citrus (Pole Evans 1911). In this publication Pole Evans mentioned that in 1903, the Government Entomologist for Natal reported great losses to the orange crop, due to a mould. He noted that he had collected the causative fungus, *P. digitatum*, from fallen oranges in the Northern Transvaal five years before (i.e in 1906). Doidge (1950) listed all *Penicillium* species recorded up to 1945, including specimens in the Collection of the Timber Research Laboratories, Chamber of Mines, Johannesburg, as well as those mentioned by Thom (1930).

The *Penicillium* specimen accessioned in the National Collection of Fungi first was '*P. armeniacum* Berk' (PREM 187—see checklist), recorded by the Government Laboratories Johannesburg, on *Zea mays* on 12 September 1906. This fungus was not a *Penicillium*, however, but probably belongs in *Monilia* (Thom 1930).

The second *Penicillium* entry, '*P. gratioti* Sartory' (PREM 5587—see checklist), was recorded by P.A. van der Bijl from the City Deep Mine in Johannesburg, on 7 December 1912. Thom (1930) provided more data about this isolate, recording its optimum temperature and utilization of various sugars. Its true identity is not clear, however, as the name is no longer in use and Raper & Thom (1949) referred to *P. gratioti* only as: 'apparently some member of the *P. janthinellum* series'.

Numerous penicillia have been reported subsequently in general surveys of fungi on various substrates. Cohen (1950) conducted the first survey of soil fungi in South Africa, comparing the effect of different burning and grazing treatments, and he recorded nine *Penicillium* species. Scott (1968a) described eight new *Eupenicillium* species from soil and included these in a more extensive monograph of the genus (Scott 1968b). *Penicillium* was found to be the genus of Fungi Imperfecti with the largest number of species represented in Zululand soil (Eicker 1969). The same locality yielded *P. olsonii* Bain. & Sartory throughout the soil profile, whereas *P. javanicum* Van Beyma showed a marked decrease with increasing soil depth (Eicker 1970). Eicker (1973) found the penicillia to have an even distribution in different litter layers of *Eucalyptus maculata* Hook. f. and later found the genus to be common on *Panicum coloratum* L. litter (Eicker 1976). *P. cyclopium* Westling was isolated from angora goat dung, but Mitchel (1970) indicated that it was probably an aerial contaminant.

High quality stored maize obtained from six localities, studied by Van der Westhuizen & Bredell (1972) was found to have a high percentage of *Penicillium* spp., with *P. oxalicum* Currie & Thom often comprising 30% of the fungi recorded. On stored lucerne seed, species of this genus did not increase during an increased period of storage (Marasas & Bredell 1973). The composition and distribution of soil fungi in the western Transvaal was studied by Papendorf (1976) and one of his isolates, described as the new species *P. striatosporum* Stolk (Stolk 1969), was later re-identified by Pitt (1979) as *P. restrictum* Gilman & Abbott. *Penicillium* spp. were found to be scarce on leaves and litter of *Cenchrus ciliaris* L. (Bezuidenhout 1977), in aerospora of an *Eragrostis curvula* (Schrad.) Nees pasture (Van der Merwe *et al.* 1979) and in the soil of Kaokoland, Namibia (Eicker *et al.* 1982). Many of the above-mentioned species are included in the checklist and bibliography of South African fungi compiled by Gorter (1979) for the period 1947–1977.

Allsop *et al.* (1987) found a more varied fungal flora present in the rhizosphere than in the non-rhizosphere area of a fynbos site; several *Penicillium* species were reported, including *P. novae-zeelandiae* Van Beyma and *Eupenicillium pinetorum* Stolk, reported in South Africa for the first time. McLean & Berjak (1987) studied the mycoflora of maize and indicated *P. variabile* Sopp as the most frequent internal contaminant of maize seed, while *P. brevicompactum* Dierckx was isolated from 15% of the seedlings. Wittaker *et al.* (1989) reported a decline in *Penicillium* species after hot water treatment of stored maize seed. penicillia were found to be present on *Eucalyptus* (Lundquist & Baxter 1985), *Pinus* in the Transvaal (Lundquist 1986), *Pinus* in the Cape (Lundquist 1987) and common on stored seed of indigenous plants (Isaacs & Benic 1990). *P. crustosum* Thom and *P. purpurescens* (Sopp) Biourge have been indicated as endophytes of grass species (De Villiers 1989). Ramirez (1990) based the description of *P. krugeri* Ramirez on 26 isolates collected from soil at different localities in the Kruger National Park in 1987.

Apparently the type material of this fungus has been lost (C. Ramirez pers. comm.).

Additional reports of South African isolates may be found in the monographs on *Penicillium* by Thom (1930), Raper & Thom (1949), Pitt (1979) and Stolk & Samson (1983), as well as in catalogues of international culture collections.

Plant pathology

During the early 1900's the deteriorators, *P. digitatum, P. expansum* Link and *P. italicum* Wehmer, became a major problem for the fruit producing industry by hampering exports to Europe (Pole Evans 1920). Most of the South African isolates mentioned by Thom (1930) had been sent to the USA for identification by V.A. Putterill. Putterill was in charge of a mycological laboratory in Cape Town in 1918, and later worked at the fruit inspection service (Doidge 1950). These first South African *Penicillium* records probably concerned fruit rot, although they are listed as having an undetermined host.

P. digitatum on citrus was reported by Pole Evans (1911) who stressed the importance of good sanitation in orchards to combat this fungus. To determine the presence of pathogenic fungal spores at the Cape harbour, Pole Evans (1920) exposed agar plates in the railway trucks and in cold storage rooms on the docks and on the ships.

These pathogens were later listed by Verwoerd (1929). Doidge & Van der Plank (1936) subsequently conducted a survey on the fungi causing rot of oranges and lemons, indicating *P. digitatum* as the most important, with *P. italicum* and *P. verrucosum* Dierckx also present. They (Doidge & Van Der Plank 1936) remarked that although a large number of additional *Penicillium* spp. were isolated during the survey, no attempt was made to identify these species which were apparently saprophytic and growing on decaying tissues. Van der Plank (1945) did experimental work with hypochlorous acid as a bleach and disinfectant of citrus fruit, finding it effective against *P. digitatum* conidia. Martin (1960) listed seven saprophytic *Penicillium* species in citrus soil and found five species in adjacent virgin soil. Other *Penicillium* species of plant pathological interest were mentioned by Doidge *et al.* (1953), Roth (1967), Wager (1972) and Gorter (1977). The bulb pathogen *P. corymbiferum* Westling, isolated by Wager, was deposited in the IMI culture collection where it was examined by Pitt (1979).

Matthee (1968) studied *P. expansum*, the pathogen and deteriorator of stored pome fruits, and indicated that older or bruised fruit was more susceptible. Holtzhausen & Knox-Davies (1974) used this fungus as an experimental organism in chemical seed treatments. Combrink *et al.* (1980) found that a longer exposure time of apples to a sodium hypochlorite solution had a better fungicidal effect on *P. expansum* conidia than a stronger solution. *P. funiculosum* Thom reportedly caused a core rot of apples and formed a moist infection (Combrink *et al.* 1985). Members of the genus were also isolated from litchi fruit (Roth 1963), bananas (Roth & Loest 1965) and mangoes (Wehner *et al.* 1981). *P. pinophilum* Hedgcock apparently enhances disease symptoms of groundnut pods in the presence of *Chalara elegans* Nag Raj & Kendrick (Baard 1988). This fungus was able to decompose filter paper as well as detached groundnut pods. Surface disinfected roots of *Medicago* spp. yielded eight different *Penicillium* spp. (Lamprecht *et al.* 1988). *P. spinulosum* Thom was found to be pathogenic on onions (Naudé & Jooste 1989) and *P. hirsutum* Dierckx on bulbs of flowering plants (Schutte 1990).

Unidentified members of the genus were reported on Japanese radish seed (Holtzhausen 1978), groundnuts (Ferreira & Lutchman 1989), recalcitrant seed (Berjak *et al.* 1989; Mycock & Berjak 1990), barley seed (Lübben *et al.* 1989) and maize cultivars (Rheeder *et al.* 1990).

Industrial applications

Penicillia encountered in industry were first reported by Van der Bijl (1920) in his study of the deterioration of cane sugar crystals and solutions in storage. This record is also of taxonomic interest as two of these *Penicillium* isolates had been sent to Thom, whose comments accompanying the identifications are included. One of these isolates was deposited in PREM: 14262 *P. luteum-purpurogenum* group.

Davel & Neethling (1930) dealt with fungi in dairies and mentioned the use of *P. camembertii* Thom, *P. glaucum* and *P. roquefortii* Thom in cheese factories, indicating that members of this group can be troublesome in these surroundings. Coles (1925) recorded *P. glaucum* on Stilton and Wenslydale cheese and Radmore (1986) did a microbiological study of air in dairies. Other work done on penicillia in the dairy industry is discussed under the heading 'Mycotoxins'.

An interesting use for *Penicillium* was found in reducing the stickiness of molasses meal (Roth 1968), for which *P. notatum* Westling was used on a commercial scale. Although photographs of eight different *Penicillium* spp. are included, only the series to which they belong are given. The wine industry noted various identified and unidentified *Penicillium* spp. on grapes (Le Roux *et al.* 1973), their incidence on healthy grapes being 60% and on *Botrytis* infected fruit 70%.

Heat resistant fungi posing problems for apple juice canners, turned out to be teleomorphs of *P. vermiculatum* Dangeard and *P. brefeldianum* Dodge (Van der Spuy *et al.* 1975). This work is referred to world-wide in connection with heat resistance of fungal spores. The thermophilic *Talaromyces dupontii* Griffen & Maublanc, was isolated during a study of fungi in mushroom compost (Eicker 1977). *Penicillium* species encountered later when various casings for mushroom production were tested, were indicated as potentially harmful (Smit 1984). Martin & Keen (1978) found *P. crustosum* to be common in home-made beer as well as on sorghum malt used for brewing. A low incidence of *Penicillium* spp. on commercial and industrial sorghum malt was reported by Rabie & Lübben (1984).

Medical importance

Although members of the genus are known to cause allergies and to produce mycotoxins, *Penicillium* is mentioned infrequently in literature on medical mycology.

Fungal allergy was the motivation for three five-year surveys of aerospora, two done in Johannesburg (Ordman & Etter 1956; Ordman 1963) and one in Windhoek (Ordman 1970). *Penicillium* made up about 10% of the fungi isolated and showed no seasonal prevalence. Fungal contamination of food was investigated by Gilman (1972), in an attempt to correlate diet and liver cancer in man and a variety of identified penicillia were listed. Antimycotic and antibacterial activity of soil fungi was studied by Eicker (1975) who found positive effects against both organisms, by *P. chrysogenum* and *P. cyclopium*. Horwitz & Wehner (1977) warned that the presence of antibiotics produced by *P. chrysogenum* Thom used in salami curing may pose a health hazard for persons sensitive to penicillin. *Penicillium* was also amongst the fungi present on corn believed to be the cause of oesophageal cancer in Transkei and in the high rate area of the disease, 43% of the samples were infected with this organism (Marasas *et al.* 1981). Marasas & Van Rensburg (1986) found this genus most prevalent on crops in the area where Mseleni joint disease occurs in Kwazulu. Some of the work mentioned under the heading 'Mycotoxins' also has a medical application.

Mycotoxins

The discovery in the 1960's of aflatoxin and its carcinogenic effects created renewed interest in fungal contamination. In the search for members of the aflatoxin-producing *Aspergillus flavus* group, numerous species of the closely related genus *Penicillium* were also encountered and details of their distribution recorded. Scott (1965), the first South African to test fungi for toxicity by feeding day old ducklings with infected meal, found *P. islandicum* Sopp, *P. oxalicum, P. rubrum* Stoll and *P. urticae* to be acutely toxic, whereas *P. piceum* Raper & Fennell had a less severe effect. This paper subsequently became a citation classic. The fungal flora of stock feeds, and the incidence of toxicity, was investigated by Van Warmelo (1967), who found that *Penicillium* had a low incidence on these substrates. Wehner & Rabie (1970) did toxicity tests with micro-organisms from nuts and dried fruit, including *P. frequentans* Westling, *P. notatum* and three unidentified *Penicillium* spp., none of which turned out to be toxic.

Martin (1974) compiled a table of all information available on mycotoxin-producing fungi, dividing them into field and storage fungi. Mutagenicity of *Penicillium* mycotoxins to *Salmonella typhimurium* was studied by Wehner *et al.* (1978) and negative results were reported for griseofulvin, patulin and penicillic acid. In a similar study, the mycotoxin emodin, produced by *P. rugulosum* Thom, was found to be a frameshift mutagen (Wehner *et al.* 1979). As no local isolates were mentioned in the above-mentioned work, the species concerned have not been included in the appended list.

The presence of mycotoxin-producing fungi on cheese was investigated by Lück *et al.* (1976) and unidentified *Penicillium* spp. were isolated from 33 out of 43 cheese samples. Some of the isolates tested had a toxic effect on ducklings. Seven isolates of *P. roquefortii*, isolated from blue cheese showed a variation in toxicity, whereas the four isolates of *P. camembertii* tested had a less pronounced effect (Lück *et al.* 1978). A noteworthy finding of Lück & Wehner (1979) was that *Penicillium* isolates grown on maize were more toxic to ducklings than those grown on milk curd. Kriek & Wehner (1981) proved the toxicity of *P. italicum*, isolated from an orange, to laboratory animals. The effect of maize meal infected with this fungus was not as detrimental to ducklings as to rats. The nature of the lesions observed in rats was similar to those caused by the toxic *P. islandicum*. Dutton & Westlake (1985) found the incidence of *Penicillium* spp. as well as contamination by its mycotoxins to be low on cereal and animal feedstuffs. Kellerman *et al.* (1988) implicated *Penicillium* as a mycotoxin producer but gave no examples. The Medical Research Council tested various isolates of 30 *Penicillium* spp. for toxicity to ducklings and found most to have a detrimental effect (C.J. Rabie pers. comm.). All isolates were identified by J.I. Pitt and are listed under the abbreviation MRC. These authors all studied the relationship between fungi and mycotoxins, but the mycotoxins themselves called for more detailed chemical studies.

Chemical work

A variety of *Penicillium* mycotoxins have been extracted and characterized in South Africa. Steyn (1969) described a new, rapid and sensitive system for the separation and detection of eleven different mycotoxins, followed by work on secalonic acid D, a toxic metabolite of *P. oxalicum* (Steyn 1970). The isolation of viridicatum toxin from *P. viridicatum* Westling was reported by Hutchison *et al.* (1973). Nagel *et al.* (1972) reported on the production of the highly toxic citreoviridin and made a study of the morphological characteristics of various isolates of its producer, *P. pulvillorum* Turfitt. Steyn *et al.* (1982) studied the biosynthesis of the above-mentioned citreoviridin.

Holzapfel (1968), Steyn *et al.* (1975), McGrath *et al.* (1976) and Neethling & McGrath (1977) studied various aspects of cyclopiazonic acid (e.g. biosynthesis, structure and production), a toxic metabolite of *P. cyclopium*. However, Frisvad (1989) stated that the isolate used for all the above-mentioned cyclopiazonic acid work, namely CSIR 1085, was not *P. cyclopium* but *P. griseofulvum* Dierckx. Pitt came to the same conclusion as indicated by De Jesus *et al.* (1981). Frisvad (1989) stated that *P. viridicatum* (CSIR 1029) used by Hutchison *et al.* (1973) had also been misidentified.

Various mycotoxins other than the above-mentioned were studied locally. Oxalin produced by *P. oxalicum* received attention from Nagel *et al.* (1976), Vleggaar & Wessels (1980) and Steyn & Vleggaar (1983), while PR toxin produced by *P. roquefortii* was studied by Gorst-Allman & Steyn (1982). Certain isolates of *P. crustosum* are able to produce tremorgenic mycotoxins and these were examined in detail by Maes *et al.* (1982) and De Jesus *et al.* (1983a, b, c). *P. janthinellum* Biourge, associated with rye grass staggers was found to produce janthitrems, tremorgenic mycotoxins studied by De Jesus *et al.* (1984). For most of these investigations the authors obtained authenticated isolates or had their fungal cultures verified, mostly by Pitt.

In 1985, South Africa hosted the IUPAC Symposium on mycotoxins and phycotoxins (Steyn & Vleggaar 1986) where a paper concerning synthesis of the *Penicillium* mycotoxins cyclopiazonic acid and viridamine was presented by Holzapfel (1986).

DISCUSSION

The large number of undetermined *Penicillium* species in the literature cited is an indication that scientists in South Africa have a history of not attempting to identify members of this genus. Other than that done by Scott (1968a, b), work published on *Penicillium* in South Africa is clearly fragmentary and many of the isolates obtained early this century were identified overseas. The use of correctly identified *Penicillium* isolates in any scientific research must be stressed. Mistaken identities have been reported for South African studies (Frisvad 1989); voucher specimens deposited in recognized culture collections will assist in overcoming this problem and will also make isolates available to other scientists.

With the exception of *P. hordei* Stolk, *P. olivicolor* Pitt and *Talaromyces stipitatus* (Thom) C. R. Benjamin, all the *Penicillium* species listed by Samson & Pitt (1985) as common, have been recorded in southern Africa. However, teleomorphic penicillia have been reported infrequently as they require special isolation techniques (Scott 1968b). Synnematous members of the genus appear to be scarce and most representatives in the National Collection of Fungi, PREM and PPRI are recent acquisitions.

The role that penicillia play in the ecology of natural ecosystems as well as in cultivated areas, has not been investigated in this country. Certain *Penicillium* species have antimycotic as well as antibacterial activities (Eicker 1975). Others are strongly antagonistic to soil-borne plant pathogens such as *Gaeumannomyces, Pythium* and *Rhizoctonia*, whereas some members of *Talaromyces* have antifungal as well as antiprotozoal capacities (Domsch *et al.* 1980). Biological control of plant pathogens by *Penicillium* species deserves attention, as it may well be of economic importance.

The successful use in *Penicillium* taxonomy of physiological and various biochemical methods, mycotoxin profiles and electron microscopy, has been indicated. However, these techniques have not yet been applied to this genus in South Africa and may be of value in determining relationships between species and groups as well as indicating new species.

Much meaningful work on *Penicillium*, one of the more common and economically important genera of fungi, is therefore still to be done in the fields of taxonomy, ecology, biological control and chemotaxonomy.

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CHECKLIST OF *PENICILLIUM, EUPENICILLIUM* AND *TALAROMYCES* SPECIES RECORDED IN SOUTHERN AFRICA

Penicillium species recorded in southern Africa up to 1990 are arranged alphabetically and the host and/or substrate from which each species has been recorded is given with the relevant literature reference. Species names are listed as cited in the original publication in roman type, with a cross reference to the epithet currently accepted by Pitt (1979) in bold, except in the case of *Eupenicillium*, where the revision proposed by Stolk & Samson (1983) has been followed, or where older epithets have been traced (Seifert & Samson 1985). In the past, ascosporic fungi were included in the genus *Penicillium*, posing nomenclatural problems ($\neq$) in designating the anamorph-teleomorph relationship. Consequently, species known to produce a teleomorphic state have been listed under *Penicillium* with a cross reference to either *Eupenicillium* or *Talaromyces*, which are listed separately.

The following abbreviations are used in the list:

CBS, South African isolates listed in the 1990 List of Cultures of the Centraalbureau voor Schimmelcultures, Baarn, The Netherlands.
IMI, cultures in the 1988 Catalogue of the Culture Collection of CAB International Mycological Institute, Kew, United Kingdom.
MRC, isolates in the Culture Collection of the Medical Research Council, all identified by Pitt (C.J. Rabie pers. comm.).
PPRI, isolates in the Culture Collection of the National Collection of Fungi. Several of these have been identified or verified by Pitt.
PREM, isolates deposited in the National Collection of Fungi as dried material.

The National Collection of Fungi recently acquired three additional fungal culture collections. Most of these cultures were no longer viable and had scant accompanying data, but local isolates are listed with numbers under their appropriate abbreviations:

CSIR, isolates listed in a collection obtained from the Council for Scientific and Industrial Research, which included some isolates of Scott (1968a, b).
MCP, the collection of Papendorf (1976), received from the University of Potchefstroom for C.H.E. These isolates are listed under the substrate soil, but some isolates could have been isolated from *Acacia karroo* litter.
UCT, a collection obtained from the University of Cape Town which contained isolates of Allsopp *et al.* (1987).

GENUS PENICILLIUM

acidoferum (see **P. canescens**)

aculeatum Raper & Fennell
cereal and legume products: Scott (1965)
soil: CSIR 348

adametzii Zaleski
Allium cepa: PREM 44729
soil: Papendorf (1976); Allsopp *et al.* (1987); MCP 35, 221, 222, 1159
ventilation tubing: Doidge (1950)
Zea mays: Van der Westhuizen & Bredell (1972)

adametzioides Abe ex G. Smith
Zea mays: McLean & Berjak (1987); PREM 47619

alutaceum (see **E. terrenum**)

arenicola Chalabuda
mushroom casing: Smit (1984)

asperum (see **E. crustaceum**)

atramentosum Thom
chicken feathers and droppings: PPRI 4086; PREM 48602
dung: PPRI 3703, 4049; PREM 49878, 50682

atrovenetum (see **P. melinii**)

armeniacum Berk (*Monilia*, Thom 1930)
Zea mays: PREM 187

aurantiobrunneum (see **P. glabrum**)

aurantiocandidum (see **P. aurantiogriseum**)

aurantiogriseum Dierckx
Arachis hypogaea: MRC 330
Aristea major: PPRI 4302
cheese: PREM 49040, 49042
Hordeum vulgare: MRC 2670
Panicum miliaceum: MRC 245
Vigna subterranea: MRC 284
Zea mays: McLean & Berjak (1987); PREM 47622
= *aurantiocandidum* Dierckx
soil: Eicker (1969, 1973)
= *cyclopium* Westling
Allium cepa: PREM 44737
Arachis hypogaea: Gilman (1972)
cereal and legume products: Scott (1965)
cheese: Lück & Wehner (1979)
dung: Mitchell (1970)
natural gum: Roth (1968)
soil: Eicker (1975); CSIR 409; MCP 378
Sorghum caffrorum: CSIR 519, 534, 542, 543
Vitis vinifera: Doidge (1950, *et al.* 1953)
Zea mays: Van der Westhuizen & Bredell (1972) CSIR 258, 303, 358, 403, 461, 462, 543, 659, 719; PREM 43751, 44302, 44303
= *johanniolii* Zaleski
undetermined host: Thom (1930)
= *lanosocoeruleum* Thom
Medicago spp.: Van Warmelo (1967)
Vitis spp.: Le Roux *et al.* (1973)
= *martensii* Biourge
Arachis hypogaea: Gilman (1972)
Zea mays: Gilman (1972); Van der Westhuizen & Bredell (1972); CSIR 660
= *solitum* Westling
material: Doidge (1950)

biforme (see **P. camembertii**)

brefeldianum (see **E. javanicum** var. **javanicum**)

brevicompactum Dierckx
aerospora: Roth (1968)
apple puree: MRC 3137
Avena sativa: MRC 2824
brattice cloth: Doidge (1950)
cereal and legume products: Scott (1965)
compost: PPRI 3186
debris: PPRI 4068
fodder: PPRI 3631
Medicago sativa: PREM 44475, 44477, 44519
natural gum: Roth (1968)
Prunus persica var. *nucipersica*: PPRI 3597
soil: Eicker (1975); CSIR 327; MCP 371

Sorghum caffrorum: CSIR 531, 547
Vitis spp.: Le Roux *et al.* (1973)
Zea mays: McLean & Berjak (1987); Pitt (1979); Van der Westhuizen & Bredell (1972); CSIR 81, 95, 219, 330, 378, 459, 593, 623, 665, 675; PPRI 3630; PREM 43741, 43742, 47537, 47831
undetermined host: CBS 287.53 (albino mutant)
= *stoloniferum* Thom
soil: Cohen (1950)
Zea mays: Van der Westhuizen & Bredell (1972); CSIR 238

camembertii Thom
cheese: Davel & Neethling (1930); Lück *et al.* (1978); PPRI 3122; PREM 47740
= *biforme* Thom
Arachis hypogaea: Van Warmelo (1967)
Medicago spp.: Van Warmelo (1967)

canescens Sopp
Barleria obtusa: PPRI 3808
flannel: PREM 33287
Protea cynaroides: PPRI 3786
soil: Papendorf (1976)
Zea mays: Van der Westhuizen & Bredell (1972)
= *acidoferum* Sopp (near **P. canescens**, Raper & Thom 1949)
Citrus sinensis: Doidge (1950)
= *kapuscinskii* Zaleski
soil: MCP 384
swine meal: Van Warmelo (1967)

capsulatum Raper & Fennell
dried fish: Pitt (1979); IMI 140 284
Medicago sativa: PREM 44469
Zea mays: CSIR 181

casei (see **P. roquefortii**)

charlesii (see **P. fellutanum**)

chermesinum Biourge
soil: Martin (1960)

chrysogenum Thom
aerospora: Roth (1968)
Arachis hypogaea: Van Warmelo (1967); PPRI 3658; PREM 48261
cereal and legume products: Scott (1965)
fishmoth gut: PREM 49016, 49017
grass: PPRI 4277
Hordeum vulgare: MRC 2807
Medicago spp.: Lamprecht (1988); PREM 48321
molasses meal: Roth (1968)
mushroom casing: Smit (1984)
natural gum: Roth (1968)
nuts and dried fruit: Wehner & Rabie (1970)
soil: Eicker (1975); Martin (1960); PREM 48767
Sorghum caffrorum: CSIR 427; MRC 1682
Zea mays: Gilman (1972); McLean & Berjak (1987); Van der Westhuizen & Bredell (1972); Van Warmelo (1967); CSIR 436, 453, 477
= *notatum* Westling
aerospora: Roth (1968)
Allium cepa: PREM 44738
Cenchrus ciliaris: Bezuidenhout (1977)
cereal and legume products: Scott (1965)
Medicago sativa: PREM 44466, 44552
molasses meal: Roth (1968)
natural gum: Roth (1968)
nuts and dried fruit: Wehner & Rabie (1970)
soil: CSIR 317, 318
Sorghum caffrorum: CSIR 285, 286
Vitis spp. Le Roux *et al.* (1973)
Zea mays: Van der Westhuizen & Bredell (1972); CSIR 265, 302, 328, 428, 434, 644
undetermined host: Doidge (1950)

citreonigrum Dierckx
mushroom casing: Smit (1984)
= *citreoviride* Biourge
Zea mays: Van der Westhuizen & Bredell (1972); CBS 239.65; CSIR 138, 505, 568, 590

citreoviride (see **P. citreonigrum**)

citrinum Thom
aerospora: Roth (1968)
Allium cepa: PREM 44777
Arachis hypogaea: Gilman (1972); MRC 241, 263, 283, 294, 2109
Avicennia spp.: PREM 47616, 47617
cereal and legume products: Scott (1965)
dried leaves: MRC 320, 333, 334
fruit: Doidge (1950); Thom (1930)
Ipomoea batatas: PPRI 3571
Manihot esculenta: MRC 212, 232, 249
Medicago spp.: Lamprecht (1988); PREM 48312
natural gum: Roth (1968)
Phaseolus spp.: MRC 178, 210, 222, 304, 313
soil: Allsopp *et al.* (1987); Cohen (1950); Eicker (1969, 1970); Papendorf (1976); CSIR 370, 372, 373, 374
Sorghum caffrorum: MRC 2332
Vigna subterranea: MRC 224, 280
Zea mays: Gilman (1972); McLean & Berjak (1987); Van der Westhuizen & Bredell (1972); CSIR 152, 352, 393, 394, 549, 661, 708; MRC 257, 258, 262, 266, 293, 294, 307, 437, 444; PREM 44304, 44305, 47620, 47621
= *steckii* Zaleski
Arachis hypogaea: Van Warmelo (1967)
cereal and legume products: Scott (1965)
soil: Eicker (1969, 1970); CSIR 346, 381, 382, 384, 385, 387
Zea mays: Van der Westhuizen & Bredell (1972); Van Warmelo (1967); CSIR 341, 383, 426, 444, 454, 595, 670; PREM 43752

claviforme (see **P. vulpinum**)

commune (see **P. puberulum**)

concentricum (see **P. coprophilum**)

coprophilum (Berk. & Curt.) Seifert & Samson
cubed dogfood: PPRI 3700
debris: PPRI 3725, 3902, 3903; PREM 49881
dung: PPRI 3726, 4107, 4128; PREM 49863, 50683, 50714
grass roots: PREM 47700
Zea mays: CBS 473.75
soil: PPRI 3611, 4280; PREM 47700, 47701
= *concentricum* Samson, Stolk & Hadlock
Zea mays: Seifert & Samson (1985)

coralligerum (see **P. herquei**)

corylophilum Dierckx
aerospora: Doidge (1950); Thom (1930)
Asparagus virgatus: PPRI 3785
contaminant: PREM 48560
lime juice: PPRI 4303
Medicago spp.: Lamprecht (1988); PREM 48316
soil: PPRI 4304
Zea mays: PREM 44307

corymbiferum (see **P. hirsutum**)

crustosum Thom
Arachis hypogaea: PREM 48018
cheese: PPRI 3892
dried fish: MRC 316
fishmoth gut: PREM 49015
Manihot esculenta: MRC 247
meat pie: MRC 1271
Oryza sativa: MRC 285
Phaseolus spp.: MRC 228
Prunus armeniacum: MRC 3015
Prunus persica: PPRI 3587
soil: Eicker (1975)
Sorghum caffrorum: Martin & Keen (1978)
Stipagrostis uniplumis: De Villiers (1989); PPRI 3457
Zea mays: Gilman (1972); Van der Westhuizen & Bredell (1972); PREM 47864

cyclopium (see **P. aurantiogriseum**)

dangeardii (see **T. flavus**)

decumbens Thom
Dalbergia obovata: PPRI 3721; PREM 49888
mushroom casing: Smit (1984)
soil: Martin (1960)
Zea mays: Van der Westhuizen & Bredell (1972); CSIR 2
undetermined host: Thom (1930)

dendriticum Pitt
contaminant: PPRI 4002; PREM 48605

debris: PPRI 3782
fodder: PPRI 3887, 4225
Protea scolopendriifolia: PPRI 4014; PREM 47704
Watsonia marginata: PPRI 3724

digitatum (Pers. ex Fr.) Sacc.
aerospora: Pole Evans (1920)
Carica papaya: Doidge (1950, *et al.* 1953)
Citrus aurantium: Doidge *et al.* (1953)
citrus fruit: Pole Evans (1911); Roth (1967)
Citrus limonia: Doidge (1950, *et al.* 1953); CSIR 562, 563; PPRI 3740
Citrus nobilis var. *deliciosa*: Doidge (1950, *et al.* 1953)
Citrus paradisi: PPRI 3319; PREM 48908
Citrus sinensis: Doidge (1950, *et al.* 1953); Doidge & Van der Plank (1936); Van der Plank (1945); Verwoerd (1929); CSIR 558, 561; PPRI 3737
soil: Eicker (1969, 1973)
= *digitatum* Sacc. var. *californicum* Thom
Physalis peruviana: Doidge *et al.* (1953)
Citrus sinensis: Doidge (1950); Doidge & Van der Plank (1936); PREM 30659

digitatum var. californicum (see **P. digitatum**)

divaricatum Thom (*Scopulariopsis*, Raper & Thom 1949)
sugar: Van der Bijl (1920)

diversum Raper & Fennell
Eucalyptus cloeziana: PPRI 3731; PREM 49865
Medicago sativa: PREM 44517

duclauxii Delacr.
aerospora: Roth (1968)
Asparagus officinalis: PPRI 4083
grass roots: PPRI 3130; PREM 47754
mine timber: Doidge (1950); Pitt (1979); Raper & Thom (1949); IMI 200 309
molasses meal: Roth (1968)
natural gum: Roth (1968)
soil: PPRI 3983, 4305; PREM 48938

dupontii (see **T. thermophilus**)

echinulatum Raper & Thom ex Fassatiová
granadilla juice: PPRI 3585

elongatum (see **P. expansum**)

erubescens (see **E. terrenum**)

expansum Link
aerospora: Pole Evans (1920)
Arachis hypogaea: Pitt (1979); MRC 199; PREM 48381
cereal and legume products: Scott (1965)
granadilla juice: PPRI 3584; PREM 49415
Malus sylvestris: Combrink *et al.* (1980); Doidge (1950, *et al.* 1953); PPRI 4215
molasses meal: Roth (1968)
natural gum: Roth (1968)
pome fruit: Matthee (1968)
Psidium guajava: PREM 48383
Strelitzia reginae: PPRI 4278
soil: CSIR 398, 410; PPRI 4279
Vigna subterranea: MRC 174
Vitis vinifera: Doidge (1950, *et al.* 1953); Le Roux *et al.* (1973); MRC 1131
Zea mays: Van der Westhuizen & Bredell (1972); CSIR 15, 71, 226, 326, 404, 443, 483, 527, 659, 717; MRC 177; PREM 47512
undetermined host: Holtzhausen & Knox-Davies (1974)
= *elongatum* Dierckx
Vitis vinifera: Doidge (1950, *et al.* 1953)

fellutanum Biourge
face cream: PPRI 4306
Protea spp.: PPRI 3980
soil: MCP 390, 391
Zea mays: Pitt (1979); CBS 268.65; IMI 162 083, 162 114; CSIR 284
= *charlesii* G. Smith
cereal and legume products: Scott (1965)
soil: Papendorf (1976); MCP 48, 117
Zea mays: Gilman (1972); Van der Westhuizen & Bredell (1972); CSIR 284, 389, 401, 476

flavidorsum (see **P. glabrum**)

frequentans (see **P. glabrum**)

funiculosum Thom
Ananas comosus: Doidge (1950, *et al.* 1953); PPRI 4307
Arachis hypogaea: Baard (1988); Gilman (1972); Pitt (1979); PPRI 3634; PREM 48015
cereal and legume products: Scott (1965)
Cyperaceae spp.: PPRI 3632; PREM 48604
Eucalyptus maculata: Eicker (1973)
Malus sylvestris: Combrink *et al.* (1985)
Medicago sativa: PREM 44513
Phaseolus spp.: MRC 281
soil: Allsopp *et al.* (1987); Doidge (1950); Eicker (1969, 1973) Martin (1960); Papendorf (1976); CSIR 141, 362, 365, 367, 368, 369; MCP 189, 336; PPRI 3504; UCT
Zea mays: Gilman (1972); McLean & Berjak (1987); Van der Westhuizen & Bredell (1972); CSIR 23, 82, 83, 92, 93, 221, 242, 300, 613; PPRI 3633; PREM 43754, 43755, 43756, 43757, 47637
undetermined host: Thom (1930); Raper & Thom (1949)
= *varians* G. Smith
Zea mays: Van Warmelo (1967)

fuscum (Sopp) Biourge (application uncertain, Pitt 1979)
Medicago sativa: PREM 44401

glabrum (Wehmer) Westling
dung: PPRI 4308
Medicago sativa: PREM 44535, 44550
Melianthus comosus: PPRI 3807
soil: Allsopp *et al.* (1987)
wine bottle cork: PPRI 3637; PREM 48406
= *aurantiobrunneum* Dierckx
soil: Cohen (1950)
= *flavidorsum* Biourge
soil: Cohen (1950)
= *frequentans* Westling
Allium cepa: PREM 44767
Arachis hypogaea: Gilman (1972)
cereal and legume products: Scott (1965)
nuts and dried fruit: Wehner & Rabie (1970)
soil: Papendorf (1976); MCP 122, 185, 190
Sorghum caffrorum: CSIR 546
Zea mays: Gilman (1972); Van der Westhuizen & Bredell (1972); Van Warmelo (1967); PREM 44300

gladioli (see **E. crustaceum**)

glandicola (Oud.) Seifert & Samson
debris: PPRI 3705; PREM 49879
fodder: PREM 48588
grass roots: PPRI 3123
= *granulatum* Bain.
aerospora: Roth (1968)
molasses meal: Roth (1968)
Triticum aestivum: MRC 1135
Zea mays: Van der Westhuizen & Bredell (1972); PREM 43750

glaucum Link (nomen confusum, Pitt 1979)
cheese: Coles (1925); Davel & Neethling (1930)
Corylus avellana: PREM 23651
nuts: Doidge (1950)

granulatum (see **P. glandicola**)

gratioti Sartory (indeterminate, Pitt 1979)
underground, gold mine: Doidge (1950); PREM 5587

griseofulvum Dierckx
birdseed: PPRI 3701
cereal and legume products: Scott (1965)
cubed dogfood: PPRI 3306, 3679
Dalbergia obovata: PPRI 3702; PREM 49887
fishmoth gut: PPRI 3123
Manihot esculenta: Pitt (1979); MRC 270, 273
Medicago spp.: Lamprecht (1988); PREM 48317, 48318
silage: CBS 315.63
soil: De Jesus *et al.* (1981); Cohen (1950); PPRI 4281
Vigna subterranea: MRC 312
Watsonia marginata: PPRI 3809
Zea mays: MRC 214
= *urticae* Bain.
cereal and legume products: Scott (1965)
soil: CSIR 391

Zea mays: PREM 44308

griseoroseum Dierckx
= *roseocitreum* Biourge
aerospora: Doidge (1950); Thom (1930)

herquei Bain & Sartory
cereal and legume products: Scott (1965)
debris: PPRI 3904
soil: Eicker (1975); CSIR 359, 360, 361, 363; PPRI 4218; PREM 48559
Zea mays: Gilman (1972); Van der Westhuizen & Bredell (1972); Van Warmelo (1967); CSIR 364, 402, 474, 538, 731
= *coralligerum* Nicot & Pionnat
soil: CSIR 1072

hirayamae (see **E. euglaucum**)

hirsutum Dierckx
Allium sativum: PPRI 3792; PREM 47862
Asparagus officinalis: PPRI 4219
Ornithogalum spp.: Pitt (1979); Schutte (1990); CBS 502.75; PPRI 3795
Gladiolus spp.: PPRI 3598, 3600, 3601, 3602; PREM 49414
= *corymbiferum* Westling
Ornithogalum spp.: Wager (1972); IMI 068 414

humuli Van Beyma
soil: Eicker (1969, 1973)
Eucalyptus maculata: Eicker (1973)

implicatum Biourge
Allium cepa: PREM 44779
Arachis hypogaea: Van Warmelo (1967)
cereal and legume products: Scott (1965)
Zea mays: Van der Westhuizen & Bredell (1972); CSIR 139, 355, 506

inflatum Stolk & Malla
soil: PPRI 3206; PREM 49071

intricatum (see **P. jensenii**)

inusitatum (see **E. inusitatum**)

islandicum Sopp
Arachis hypogaea: Gilman (1972)
cereal and legume products: Scott (1965)
contaminant: PPRI 3124, 3714; PREM 47753, 49869
Sorghum caffrorum: Rabie & Lübben (1984)
Zea mays: Gilman (1972); Van der Westhuizen & Bredell (1972)
undetermined host: Raper & Thom (1949); Thom (1930); CBS 176.68

italicum Wehmer
aerospora: Pole Evans (1920)
Citrus sinensis: Doidge *et al*. (1953); Doidge & Van der Plank (1936); Verwoerd (1929)
Citrus limonia: Doidge (1950, *et al*. 1953)
Citrus maxima: Doidge (1950, *et al*. 1953)
Citrus nobilis var. *deliciosa*: Doidge (1950); PPRI 3723; PREM 48607
Citrus sinensis: Doidge (1950); Kriek & Wehner (1981); IMI 78 681; PPRI 4309; PREM 48606
fodder: PREM 48386, 48389
mushroom casing: Smit (1984)
Prunus persica: Doidge (1950)
Prunus salicina: Doidge (1950)

janczewskii Zaleski
Barleria obtusa: PREM 49890
contaminant: PREM 47702
Encephalartos laevifolius: PPRI 3179
Medicago spp.: Lamprecht (1988); PREM 48320
Pinus elliottii: PREM 48907
soil: Allsopp *et al*. (1987); Eicker (1969); PPRI 3586
undetermined host: CBS 384.67
= *nigricans* Bain.
cereal and legume products: Scott (1965)
Medicago sativa: PREM 44523
soil: Martin (1960); CSIR 325
Sorghum caffrorum: MRC 1552
Zea mays: Van der Westhuizen & Bredell (1972); Van Warmelo (1967)

janthinellum Biourge
Arachis hypogaea: PREM 48262
brattice cloth: Doidge (1950)
cereal and legume products: Scott (1965)
Medicago spp.: Lamprecht (1988); PREM 48319
soil: CSIR 319, 320, 321, 322, 340, 342; MCP 365; PREM 48013, 48014, 48905
Zea mays: McLean & Berjak (1987); Van der Westhuizen & Bredell (1972); PREM 47545

javanicum (see **E. javanicum** var. **javanicum**)

jensenii Zaleski
Allium cepa: PREM 44761
mushroom casing : Smit (1984)
soil: Eicker (1969, 1970); PREM 44256
Zea mays: Van der Westhuizen & Bredell (1972), PREM 43740, 43753
= *intricatum* Thom
soil: Cohen (1950)
flannel: Doidge (1950)

johannioli (see **P. aurantiogriseum**)

kapuscinskii (see **P. canescens**)

krugeri Ramirez
soil: Ramirez (1990)

lanosocoeruleum (see **P. aurantiogriseum**)

lanosum (see **P. puberulum**)

lapidosum (see **E. lapidosum**)

lilacinum Thom (*Paecilomyces lilacinus*, Pitt 1979)
soil: Martin (1960); Papendorf (1976)
swine meal: Van Warmelo (1967)
Zea mays: Van der Westhuizen & Bredell (1972)

lividum Westling
debris: PPRI 3707; PREM 49886
soil: PPRI 4043

luteum (see **T. luteus**)

luteoviride Biourge (indeterminate, Pitt 1979)
aerospora: Doidge (1950); Thom (1930)

martensii (see **P. aurantiogriseum**)

megasporum Orput & Fennell
Encephalartos laevifolius: PREM 49069

melinii Thom
debris: PREM 47699
Encephalartos laevifolius: PPRI 3178; PREM 49070
mouse nest material: PPRI 4223
mushroom casing: Smit (1984)
soil: Allsopp *et al*. (1987); Pitt (1979); PPRI 4042; PREM 47699
= *atrovenetum* G. Smith
Arachis hypogaea: CBS 240.65
Zea mays: Van der Westhuizen & Bredell (1972); CSIR 323, 324

meridianum (See **E. meridianum**)

miczynskii Zaleski
debris: PPRI 3710; PREM 49882
soil: Allsopp *et al*. (1987); PPRI 4040
Zea mays: MRC 426
undetermined host: Pitt (1979)
= *pedemontanum* Mosca & Fontana
soil: Papendorf (1976); MCP 127
Zea mays: PREM 44301
= *soppii* Zaleski
Eucalyptus maculata: Eicker (1973)
soil: Eicker (1969, 1970, 1973); PREM 44281
undetermined host: CSIR 1398

minioluteum Dierckx
Dianthus caryophyllus: PPRI 3982
Hordeum vulgare: MRC 1756
paper: PPRI 3659; PREM 49874
soil: PREM 48586, 48587
Zea mays: McLean & Berjak (1987); PPRI 3984, 4020; PREM 47533, 47538, 47539, 47544, 47618

montanense Christensen & Bakus
soil: PPRI 4041

multicolor (see **P. sclerotiorum**)

nigricans (see **P. janczewskii**)

notatum (see **P. chrysogenum**)

novae-zeelandiae Van Beyma
Protea spp.: PPRI 3978
soil: Allsopp *et al.* (1987); PPRI 4222

ochrochloron Biourge
soil: Eicker (1969)

ochrosalmoneum (see **E. ochrosalmoneum**)

olivinoviride (see **P. viridicatum**)

olsonii Bain. & Sartory
debris: PPRI 4038
Eucalyptus maculata: Eicker (1973)
Gloxinia spp. PPRI 3706
mushroom casing: Smit (1984)
soil: Eicker (1969, 1970, 1973)
Tribulus terrestris: PPRI 3308; PREM 49207
Zea mays: PREM 47861, 47863

oxalicum Currie & Thom
Aloe asperifolia: MCP 351
Arachis hypogaea: PREM 48260, 48567
cereal and legume products: Scott (1965)
debris: PPRI 4039
dried fish: MRC 322
face cream: PPRI 3272
fodder: PREM 48584, 48585
soil: CSIR 331, 332, 333, 335, 338
Sorghum caffrorum: CSIR 296, 522, 523
Zea mays: Doidge (1950); McLean & Berjak (1987); Nagel *et al.* (1976); Steyn (1970); Van der Westhuizen & Bredell (1972); CSIR 210, 293, 368, 504, 555, 589, 615, 620, 643, 650, 676; PREM 47542

palitans (see **P. viridicatum**)

paraherquei (see **P. simplicissimum**)

paxilli Bain.
Encephalartos laevifolius: PPRI 3183, 3184
mouse nest material: PPRI 4220

pedemontanum (see **P. miczynskii**)

petchii Sartory & Bain. (indeterminate, Pitt 1979)
Ananas comosus: Doidge (1950)

piceum Raper & Fennell
cereal and legume products: Scott (1965)
debris: PPRI 4019; PREM 49864
soil: CSIR 345

pinetorum (see **E. pinetorum**)

pinophilum Hedgcock
Ananas comosus: Doidge (1950)
Arachis hypogaea: Baard (1988); PPRI 3661; PREM 48033, 48384, 48385
compost: PPRI 3166; PREM 49030
Ehretia rigida: PPRI 4310
Sorghum caffrorum: MRC 1587
Zea mays: PREM 47638
undetermined host: Thom (1930)
= *purpurogenum* var. *rubisclerotium* Thom
cereal and legume products: Scott (1965)
Zea mays: CSIR 72, 90, 100, 207, 233, 277, 329, 366, 524

piscarium (see **P. simplicissimum**)

primulinum Pitt
Eucalyptus cloeziana: PPRI 3730; PREM 49866

puberulum Bain.
Allium cepa: PREM 44765
Arachis hypogaea: Pitt (1979); MRC 335
Encephalartos laevifolius: PPRI 3205
soil: PPRI 3204
Zea mays: Van der Westhuizen & Bredell (1972)
= *commune* Thom
aerospora: Roth (1968)
Cenchrus ciliaris: Bezuidenhout (1977)
flannel: PREM 33289
molasses meal: Roth (1968)
Zea mays: Van der Westhuizen & Bredell (1972)
= *lanosum* Westling
brattice cloth: Doidge (1950)
cheese: Lück & Wehner (1979)
soil: Papendorf (1976); MCP 163
Zea mays: Gilman (1972)

pulvillorum (see **P. simplicissimum**)

purpurescens (Sopp) Biourge
Fingerhuthia africana: De Villiers (1989); PREM 49278
mushroom casing: Smit (1984)
Protea spp.: PPRI 4284
stored foods: IMI 141 658
Vitis vinifera: PPRI 3574

purpurogenum Stoll
aerospora: Roth (1968)
Agave sisalana: PREM 48893
Allium cepa: PPRI 4224; PREM 44773
Arachis hypogaea: Gilman (1972); CSIR 13
Manihot esculenta: Pitt (1979); MRC 181
molasses meal: Roth (1968)
natural gum: Roth (1968)
nuts and dried fruit: Wehner & Rabie (1970)
Phaseolus spp.: MRC 182
soil: Allsopp *et al.* (1987); CSIR 350, 351
Sorghum caffrorum: MRC 2501
sugar: Doidge (1950); Van der Bijl (1920)
Vitis spp.: Le Roux *et al.* (1973)
Zea mays: Gilman (1972); Van der Westhuizen & Bredell (1972); MRC 315; PPRI 3120, 3783; PREM 49018
= *rubrum* Stoll
Arachis hypogaea: CSIR 13
cereal and legume products: Scott (1965)
cheese: Lück & Wehner (1979)
Medicago sativa: PREM 44370
Zea mays: Gilman (1972); Van der Westhuizen & Bredell (1972); PREM 43747

purpurogenum var. rubisclerotium (see **P. pinophilum**)

pusillum (see **E. cinnamopurpureum**)

putterillii Thom (*Geosmithia putterillii*, Pitt 1979)
aerospora: Doidge (1950); Thom (1930)

raciborskii Zaleski
aerospora: PPRI 3712; PREM 49885
Arachis hypogaea: PPRI 3664
soil: Stolk & Samson (1983); PPRI 4217
Watsonia marginata: PPRI 3722
= *raistrickii* G. Smith
Arachis hypogaea: Pitt (1979); MRC 197
cereal and legume products: Scott (1965)
mushroom casing: Smit (1984)
soil: Allsopp *et al.* (1987); CSIR 388
Sorghum caffrorum: CSIR 526, 528, 529, 545
Zea mays: McLean & Berjak (1987); Van der Westhuizen & Bredell (1972); CSIR 4; PREM 47636

raistrickii (see **P. raciborskii**)

restrictum Gilman & Abbott
Acacia karroo: Pitt (1979)
Helianthus annuus: PREM 47856
soil: Allsopp *et al.* (1987); Papendorf (1976); MCP 23
= *striatisporum* Stolk
Acacia karroo: Stolk (1969); IMI 151 749
soil: Stolk (1969); Papendorf (1976); MCP 116, 213

roquefortii Thom
cheese: Davel & Neethling (1930); Doidge (1950); Lück *et al.* (1978); CSIR 390, 392, 423, 447, 450, 455, 493, 497, 498, 499, 502, 503, 507, 509, 510, 512; PREM 49041, 49050; PPRI 3167, 3190, 3889; UCT
Medicago spp.: Lamprecht (1988); PPRI 3125; PREM 48315
Vitis spp.: Le Roux *et al.* (1973)
Zea mays: Van der Westhuizen & Bredell (1972); Van Warmelo (1967)
= *casei* Staub
soil: Eicker (1969, 1970, 1973); PREM 44280

roseocitreum (see **P. griseoroseum**)

roseopurpureum Dierckx
soil: Papendorf (1976)

Zea mays: CSIR 400

rubrum (see **P. purpurogenum**)

rugulosum Thom
aerospora: Roth (1968)
Allium cepa: PREM 44775
Arachis hypogaea: PREM 48388
coconut matting: Doidge (1950)
Gladiolus spp.: PPRI 3596; PREM 49413
natural gum: Roth (1968)
Zea mays: Van der Westhuizen & Bredell (1972); PREM 43739
= *tardum* Thom
aerospora: Doidge (1950); Thom (1930)
Arachis hypogaea: Gilman (1972)
soil: CSIR 344; MCP 372
timber: Doidge (1950)
Zea mays: Gilman (1972); Van der Westhuizen & Bredell (1972)

sclerotiorum Van Beyma
fodder: PREM 48876
Kniphofia spp.: PREM 48877
soil: Pitt (1979); Raper & Thom (1949); PREM 48571; PPRI 3901, 4069, 4139
Zea mays: Stolk & Samson (1983); MRC 425
= *multicolor* Grigorieva-Manoilova & Poradielova (application uncertain, Pitt 1979)
cereal and legume products: Scott (1965)
Eucalyptus maculata: Eicker (1973)
soil: Eicker (1969, 1973, 1975); Papendorf (1976)
Zea mays: Van der Westhuizen & Bredell (1972); CSIR 208, 397; MCP, PREM 43748

senticosum (see **E. senticosum**)

simplicissimum (Oudem.) Thom
Arachis hypogaea: PREM 48032, 48564
cereal and legume products: Scott (1965)
dung: PPRI 3214; PREM 49084
flannel bag: Raper & Thom (1949); Pitt (1979); IMI 039 816
Medicago spp.: Lamprecht *et al.* (1988); PREM 48313, 48314
soil: Eicker (1969); Papendorf (1976); CSIR 339; MCP 178, 179; PPRI 4067; PREM 48902, 48903, 48904
Sorghum caffrorum: MRC 2206
ventilation tubing: Doidge (1950)
Zea mays: Van der Westhuizen & Bredell (1972); CSIR 77
= *paraherquei* Abe
soil: Papendorf (1976); MCP 39, 105, 188
= *piscarium* Westling
soil: Papendorf (1976); MCP 187
= *pulvillorum* Turfitt
cereal and legume products: Scott (1965)
Eucalyptus maculata: Eicker (1973)
soil: Eicker (1969, 1973); PREM 44287
Zea mays: Nagel & Steyn (1972); CSIR 1405, 1406

solitum (see **P. aurantiogriseum**)

soppii (see **P. miczynskii**)

spiculisporum (see **T. trachyspermus**)

spinulosum Thom
Allium cepa: Naude & Jooste (1989); PREM 48012, 48561, 48871, 48872, 48873
Pinus spp.: PPRI 3505
soil: Cohen (1950); Papendorf (1976); MCP 165; UCT
Zea mays: Van der Westhuizen & Bredell (1972); CSIR 200; PREM 43749
undetermined host: Thom (1930)
= *terlikowskii* Zaleski
Zea mays: CSIR 411, 412, 475, 684, 685
= *trzebinskii* Zaleski
soil: Cohen (1950)

steckii (see **P. citrinum**)

stolkiae (see **E. stolkiae**)

stoloniferum (see **P. brevicompactum**)

striatisporum (see **P. restrictum**)

sublateritium Biourge
soil: Cohen (1950)

tardum (see **P. rugulosum**)

terlikowskii (see **P. spinulosum**)

terrenum (see **E. terrenum**)

terrestre Raper & Thom (application uncertain, Pitt 1979)
Zea mays: Van der Westhuizen & Bredell (1972)

thomii Maire
aerospora: Roth (1968)
cereal and legume products: Scott (1965)
Cussonia paniculata: PPRI 3784
molasses meal: Roth (1968)
soil: Eicker (1975); Papendorf (1976); CSIR 752; MCP 38; PPRI 3237, 4044; UCT
Zea mays: Van der Westhuizen & Bredell (1972)

trzebinskii (see **P. spinulosum**)

urticae (see **P. griseofulvum**)

variabile Sopp
Allium cepa: PREM 44757, 44764
Arachis hypogaea: Gilman (1972)
cereal and legume products: Scott (1965)
coconut matting: Raper & Thom (1949); IMI 040 040
Hordeum vulgare: MRC 1755
leaves: MRC 319
Medicago sativa: PREM 44547, 44548
paper: PPRI 3657; PREM 49876
soil: CSIR 206, 353, 356, 467
Vitis spp.: Le Roux *et al.* (1973)
Zea mays: Gilman (1972); McLean & Berjak (1987); Van der Westhuizen & Bredell (1972); Van Warmelo (1967); CSIR 70, 73, 232, 269, 296, 395, 464, 472, 548; PREM 43743, 43744, 43745, 43746, 47540, 47541, 47543

varians (see **P. funiculosum**)

velutinum Van Beyma
Eucalyptus maculata: Eicker (1973)
Medicago sativa: PREM 44522, 44549
soil: Eicker (1969, 1970, 1973); PREM 44260
Zea mays: Van der Westhuizen & Bredell (1972) PREM 44306, 47514

vermiculatum (see **T. flavus**)

verrucosum Dierckx
cheddar cheese: Pitt (1979)
Citrus sinensis: Doidge (1950, *et al.* 1953); Doidge & Van der Plank (1936)
debris: PPRI 3121
Phaseolus spp: MRC 220
soil: PPRI 3575

verruculosum Peyronel
Casuarina spp.: PREM 47707
Eucalyptus maculata: Eicker (1973)
Oryza sativa: MRC 171
soil: Allsopp *et al.* (1987); Eicker (1969, 1970, 1973); CSIR 347; PPRI 3501; PREM 44265, 48017; UCT
Zea mays: PPRI 3837

viridicatum Westling
aerospora: Thom (1930); Doidge (1950)
Arachis hypogaea: MRC 292
birdseed: PREM 4221
cereal and legume products: Scott (1965)
cheese: MRC 1132
Hordeum vulgare: MRC 1761, 2669, 2830
material: Doidge (1950)
natural gum: Roth (1968)
soil: CSIR 15, 405, 407; PREM 48906
Zea mays: Hutchison *et al.* (1973); Pitt (1979); Van der Westhuizen & Bredell (1972); CSIR 255, 349, 354, 396, 413, 425, 430, 460, 570, 663, 724; MRC 422
= *olivinoviride* Biourge
Allium cepa: PREM 44769
= *palitans* Westling
Allium cepa: PREM 44758
flannel: Doidge (1950)
Zea mays: Van der Westhuizen & Bredell (1972)

vulpinum (Cooke & Massee) Siefert & Samson
dung: PPRI 3727; PREM 49880
= *claviforme* Bain.

molasses meal: Roth (1968)
soil: CSIR 1088, 1089

waksmanii Zaleski
Barleria obtusa: PPRI 3704; PREM 49884
Encephalartos spp.: PPRI 4283
Medicago sativa: PREM 44474
mushroom casing: Smit (1984)
soil: Eicker (1975); Papendorf (1976); MCP 40
Zea mays: Van der Westhuizen & Bredell (1972); MRC 203

wortmannii (see **T. wortmannii**)

Penicillium species undetermined
aerospora: Ordman (1963, 1970); Ordman & Etter (1956); Radmore (1986); Van der Merwe *et al.* (1979)
Arachis hypogaea: Ferreira & Lutchman (1989); Marasas & Van Rensburg (1986); Van Warmelo (1967)
Cenchrus ciliaris: Bezuidenhout (1977)
cheese: Lück *et al.*(1976); Lück & Wehner (1979)
Citrus sinensis: Doidge (1950); Doidge & Van der Plank (1936); Roth (1967); Verwoerd (1929)
Crucifera spp.: Holtzhausen & Knox-Davies (1974)
Cucumis melo: Doidge *et al.* (1953)
Eucalyptus spp.: Lundquist & Baxter (1985)
fodder: Dutton & Westlake (1985)
foodstuff: Martin & Keen (1978)
Hordeum vulgare: Lübben & Rabie (1989)
indigenous seed: Isaacs & Benic (1990)
Iris spp.: Doidge *et al.* (1953)
Litchi chinensis: Doidge *et al.* (1953); Roth (1963)
Lupinus spp.: Van Warmelo (1967)
Mangifera indica: Wehner *et al.* (1981)
Malus sylvestris: Doidge *et al.* (1953); Verwoerd (1929)
Medicago sativa: Lamprecht (1988); Marasas & Bredell (1973); Van Warmelo (1967); PREM 44530, 44551, 44554
molasses meal: Roth (1968)
Musa spp.: Roth & Loest (1965)
mushroom casing: Smit (1984)
Narcissus spp.: Doidge *et al.* (1953)
nuts and dried fruit: Wehner & Rabie (1970)
Panicum coloratum: Eicker (1976)
Pinus spp.: Lundquist (1987)
Prunus persica: Doidge *et al.* (1953)
Prunus salicina: Doidge *et al.* (1953)
recalcitrant seed: Berjak *et al.* (1989); Mycock & Berjak (1990)
Raphanus sativus var. *longipinnatus*: Holtzhausen (1978)
Saccharum officinarum: Doidge (1950)
smoked shrimps: Gilman (1972)
soil: Allsopp *et al.* (1987); Cohen (1950); Eicker (1975, *et al.* 1982); Papendorf (1976); CSIR 312
Sorghum caffrorum: Rabie & Lübben (1984); CSIR 316, 521, 533
Tulipa spp.: Doidge *et al.* (1953)
Vitis spp.: Le Roux *et al.* (1973); Verwoerd (1929)
Zea mays: Gilman (1972); Marasas *et al.* (1981); Marasas & Van Rensburg (1986); McLean & Berjak (1987); Van Warmelo (1967); Wittaker *et al.* (1989); CSIR 218, 264, 414, 415

GENUS EUPENICILLIUM

alucateum (see **E. terrenum**)

anatolicum (see **E. euglaucum**)

baarnense (Van Beyma) Stolk & Scott
Acacia mollesjuna: CBS 339.61
soil: Scott (1968b), CSIR 1059, 1070, 1071, 1090, 1106, 1107, 1130; PPRI 3259

brefeldianum (see **E. javanicum** var. **javanicum**)

catenatum Scott
soil: Scott (1968a); Stolk & Samson (1983); CBS 325.67; CSIR 1097; PREM 48556

cinnamopurpureum Scott & Stolk
Pinus spp.: CBS 492.66; CSIR 946
soil: Scott (1968b); Stolk & Samson (1983); CBS 490.66, 491.66; CSIR 942, 943, 945, 946, 1126; PREM 48558
Zea mays: Stolk & Samson (1983)
undetermined host: Stolk & Samson (1983)
≠ *P. pusillum* G. Smith
Zea mays: CSIR 606

crustaceum Ludwig
soil: Scott (1968b), CBS 214.71, 215.71, 216,71; CSIR 1026, 1027, 1057, 1102, 1105, 1124; PREM 48551
≠ *P. asperum* (Shear) Raper & Thom
Eucalyptus maculata: Eicker (1973)
soil: Eicker (1969, 1970, 1973); PREM 44264
≠ *P. gladioli* McCulloch & Thom
Gladiolus spp.: Doidge (1950, *et al.* 1953); PREM 30706

ehrlichii (see **E. javanicum** var. **javanicum**)

erubescens (see **E. terrenum**)

euglaucum (Van Beyma) Stolk & Samson
soil: Stolk & Samson (1983); CBS 467.67
Zea mays: Stolk & Samson (1983); CBS 238.65
= *anatolicum* Stolk
soil: Scott (1968b); Stolk & Samson (1983) CSIR 1095, 1113
= *hirayamae* Scott & Stolk
soil: Allsopp *et al.* (1987); Scott (1968b); CSIR 1112; PPRI 3264; PREM 49212
Zea mays: CBS 238.65; CSIR 445
≠ *P. hirayamae* Scott & Stolk
Zea mays: CSIR 487, 554; IMI 136 205

hirayamae (see **E. euglaucum**)

inusitatum Scott
soil: Scott (1968a); Stolk & Samson (1983); CBS 351.67; CSIR 1096; PREM 48570
≠ *P. inusitatum* Scott
soil: IMI 136 214

javanicum (Van Beyma) Stolk & Scott var. **javanicum**
apple juice: Stolk & Samson (1983)
soil: Stolk & Samson (1983); CBS 211.71
undetermined host: Stolk & Samson (1983)
= *brefeldianum* (B. Dodge) Stolk & Scott
apple juice: CBS 291.62
soil: Scott (1968b); Stolk & Samson (1984), CBS, CSIR 1002, 1010, 1011, 1012, 1013; 1028, 1029, 1030, 1068, 1069, 1108, 1109; PPRI 3260; PREM 48555
undetermined host: Stolk & Samson (1983)
≠ *P. brefeldianum* B. Dodge
apple juice: Van der Spuy *et al.* (1975)
= *ehrlichii* (Klebahn) Stolk & Scott
soil: Scott (1968b), CSIR 1025, 1026, 1027; MCP, ; PPRI 3262, 3695; PREM 49195, 49362
= *javanicum* (Van Beyma) Stolk & Scott
Arachis hypogaea: CSIR 416, 417, 419, 420, 421, 424; PREM 48259
soil: Scott (1968b), CSIR 1004, 1005, 1006, 1007, 1008, 1009, 1015, 1018, 1019, 1025, 1026, 1027, 1110; 48382, 48550;
≠ *P. javanicum* Van Beyma
soil: Eicker (1969, 1970, 1973); Martin (1960); Papendorf (1976); MCP 123
Zea mays: Van der Westhuizen & Bredell (1972)

lapidosum Scott & Stolk
soil: Scott (1968b); CBS 318.66, CSIR 1035; PREM 48880
Zea mays: CSIR 1093
unrecorded host: Stolk & Samson (1983)
≠ *P. lapidosum* Raper & Fennell
soil: IMI 113 748; PREM 48880; UCT

meridianum Scott
soil: Scott (1968a, b); Stolk & Samson (1983); CBS 314.67, 217.71, 219.71; CSIR 1052, 1037, 1036, 1103; PREM 48884
≠ *P. meridianum* Scott
soil: IMI 136 209

ochrosalmoneum Scott & Stolk
soil: Scott (1968b), Stolk & Samson (1983); CBS 515.67; CSIR 1094; PREM 48886
Zea mays: Stolk & Samson (1983); CBS 489.66; CSIR 145
≠ *P. ochrosalmoneum* Udagawa
Zea mays: IMI 116 248

parvum (Raper & Fennell) Stolk & Scott
soil: Scott (1968b), CSIR 973, 1054, 1058; MCP, PPRI 3263; PREM 48557, 48881, 48887, 49194

pinetorum Stolk
soil: Allsopp *et al.* (1987); Scott (1968b); CBS 328.71; CSIR 1092, 1125; PPRI 3490; PREM 48883; UCT

≠ *P. pinetorum* Stolk
soil: CSIR 1092

senticosum Scott
soil: Scott (1968a, b); Stolk & Samson (1983); CBS 313.67, 329.71; CSIR 1042, 1104; IMI 216 905; PREM 48882
≠ *P. senticosum* Scott
soil: IMI 216 905

shearii Stolk & Scott
Medicago spp.: Lamprecht (1988); PPRI 4017; PREM 48322
soil: Scott (1968b); CSIR 1003, 1016, 1017; PREM 48549
Zea mays: CSIR 722

stolkiae Scott
soil: Scott (1968a, b); Stolk & Samson (1983); CBS 315.67, 330.71, 331.71; CSIR 1003, 1041, 1074; PREM 48552
≠ *P. stolkiae* Scott
soil: IMI 136 210

terrenum Scott
soil: Scott (1968a, b), Stolk & Samson (1983); CBS 313.67, 212.71, 213.71, 220.71, 327.71; CSIR 972, 1020, 1021, 1022, 1023, 1024; PPRI 3266
= *alutaceum* Scott
soil: Scott (1968a); Stolk & Samson (1983); CBS 317.67; CSIR 1039, 1056, 1091, 1100, 1101; PPRI 3488; PREM 48885
= *erubescens* Scott
soil: Scott (1968a, b); Stolk & Samson (1983); CBS 318.67, 319.67; CSIR 944, 974, 1040, 1032, 1034, 1038, 1040, 1061; PPRI 3261; PREM 48554, 49199
≠ *P. alutaceum* Scott
soil: IMI 136 243
≠ *P. erubescens* Scott
soil: IMI 136 404
≠ *P. terrenum* Scott
soil: IMI 136 208

Eupenicillium species undetermined
mushroom casing: Smit (1984)
soil: CSIR 1127, 1128, 1129; PPRI; UCT

GENUS TALAROMYCES

avellaneus (Thom & Turesson) C.R. Benjamin (anamorph: *Merimbla ingelheimense*, Pitt 1979)
soil: CSIR 958, 959

bacillosporus (Swift) C.R Benjamin (anamorph: *Geosmithia swiftii*, Pitt 1979)
soil: CSIR 961

flavus (Klöcker) Stolk & Samson
apple juice: Pitt (1979)
contaminant: PPRI 3790; PREM 48577
Encephalartos laevifolius: PPRI 3213; PREM 49074
wine bottle cork: MCP 27
= *flavus* var. *macrosporus* Stolk & Samson
fruit: Stolk & Samson (1972); CBS 317.63; IMI 197 487
soil: Stolk & Samson (1972); CBS 226.72; PPRI 3791
= *vermiculatus* (Dang.) C.R. Benjamin
soil: CSIR 960, 962, 963
≠ *P. dangeardii* Pitt
apple juice: IMI 197 478
≠ *P. vermiculatum* Dang.
apple juice: Van der Spuy *et al.* (1975)
soil: Eicker (1969, 1973)

luteus (Zukal) C.R. Benjamin
≠ *P. luteum* Zukal
aerospora: Roth (1968)
Citrus sinensis: Doidge (1950)
flannel: Doidge (1950); PREM 33288
molasses meal: Roth (1968)
natural gum: Roth (1968)

spiculisporus (see **T. trachyspermus**)

thermophilus Stolk
Celtis africana litter: Pitt (1979); Stolk & Samson (1972); CBS 116.72
≠ *P. dupontii* Griffin & Maubl.
apple juice: Van der Spuy *et al.* (1975)
compost: IMI 197 483
mushroom compost: Eicker (1977)

trachyspermus (Shear) Stolk & Samson
Manihot esculenta: Pitt (1979); MRC 724
contaminant: PPRI 3885
= *spiculisporus* (Lehman) C.R. Benjamin
soil: CSIR 955, 956
≠ *P. spiculisporum* Lehman
undetermined host: MCP 1125

vermiculatus (see **T. flavus**)

wortmannii (Klöcker) C.R. Benjamin
Arachis hypogaea: MRC 332
Oryza sativa: Pitt (1979)
soil: Allsopp *et al.* (1987); MCP 1134; Stolk & Samson (1972); CBS 293.53; CSIR 954, 957, 964, 965
Watsonia marginata: PPRI 3675
≠ *P. wortmannii* Klöcker
Oryza sativa: MRC 243

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Vegetation and checklist of Inaccessible Island, central South Atlantic Ocean, with notes on Nightingale Island

J.P. ROUX*, P.G. RYAN**, S.J. MILTON*** and C.L. MOLONEY**

Keywords: Inaccessible Island, Nightingale Island, south Atlantic ocean, vegetation

ABSTRACT

The physiography and climate of Inaccessible and Nightingale Islands are briefly discussed. The vegetation and the major plant associations are described. Notes are given on the ecology and distribution of each taxon. Taxa newly recorded for Inaccessible Island include *Agrostis goughensis, A.holgateana, A. wacei, Calamagrostis deschampsiiformis, Carex thouarsii* var. *recurvata, Conyza albida, Elaphoglossum campylolepium* and *Uncinia meridensis*. One species, *C. albida*, is alien to the Tristan group. Two native ferns *Asplenium platybasis* var. *subnudum* and *Blechnum australe* were found on Nightingale Island for the first time, and the presence of introduced *Malus domestica* orchards was recorded. Two unidentified taxa were found that may represent new species: *Elaphoglossum* sp. at Inaccessible Island and *Apium* sp. at both Inaccessible and Nightingale Islands.

The total number of vascular plant species recorded at Inaccessible and Nightingale Islands now stands at 98 and 43, respectively, of which 26 (28%) and seven (16%) are introduced species. Only *Atriplex plebeja* and two species of *Cotula* occur at Nightingale Island but are absent from Inaccessible Island.

UITTREKSEL

Die fisiografie, klimaat en plantgemeenskappe van Inaccessible- en Nightingale-eilande, word kortliks beskryf. Inligting oor die ekologie en verspreiding van elke takson word ook verskaf. Agt taksons, *Agrostis goughensis, A. holgateana, A. wacei, Calamagrostis deschampsiiformis, Carex thouarsii* var. *recurvata, Conyza albida, Elaphoglossum campylolepium* en *Uncinia meridensis* word almal die eerste keer op Inaccessible-eiland aangeteken. *C. albida* is 'n indringer in die Tristan-groep. Nuwe verspreidings vir Nightingale-eiland sluit onder meer die twee varingspesies *Asplenium platybasis* var. *subnudum* en *Blechnum australe* en gevestigde appelboorde, *Malus domestica*, in. Twee ongeïdentifiseerde taksons wat moontlik nuwe spesies mag wees, is versamel: *Elaphoglossum* sp. op Inaccessible-eiland en *Apium* sp. op beide Inaccessible- en Nightingale-eilande.

Die totale aantal vaatplantspesies wat op Inaccessible- en Nightingale-eilande aangeteken is, staan nou onderskeidelik op 98 en 43, waarvan 26 (28%) en sewe (16%) indringers is. *Atriplex plebeja* en twee *Cotula*-spesies is die enigste plante wat op Nightingale-eiland voorkom maar van Inaccessible-eiland afwesig is.

INTRODUCTION

Inaccessible and Nightingale Islands are uninhabited islands in the Tristan da Cunha group, central South Atlantic Ocean. Situated at 37°S, they are among the temperate oceanic islands least disturbed by human activities (Wace & Holdgate 1976). Several botanical collections have been made on the islands despite the hazardous landing conditions, but most collections were scant, resulting from short visits only (Groves 1981). The most recent floristic account of the floras at Inaccessible and Nightingale Islands is that of Wace & Dickson (1965). We provide a more complete and up-to-date account of the vegetation of the two islands as a result of a summer-long stay on Inaccessible Island between October 1989 and March 1990. Nightingale Island was visited on one day in October, two days in November and one day in December.

GEOLOGY, PHYSIOGRAPHY AND CLIMATE

Inaccessible and Nightingale Islands are of volcanic origin, associated with the Mid-Atlantic Ridge. Bathymetric surveys of the coastal waters suggest that the islands are remnants of once much larger islands (Baker *et al.* 1964). Lavas from Inaccessible Island have been dated at approximately three million years old, whereas Nightingale Island originated approximately 18 million years ago (Gass 1967; McDougall & Ollier 1982). The geology of the islands has been described by Baker *et al.* (1964). Inaccessible Island consists of thin basaltic lava flows interbedded with ash and cinders, with intrusive trachyte dykes, plugs and domes. Nightingale Island, being older, is more extensively eroded, and consists almost entirely of trachytes.

Inaccessible Island has a planar area of approximately 12 km^2 (Preece *et al.* 1986, *contra* Siddall 1985). It is surrounded by sheer cliffs which are 500 m high in the west and 200 m in the east (Figure 1). The plateau is undulating, with three main drainage basins and a few small hills, the highest being Swale's Fell, 511 m (Figure 2). Nightingale Island has a planar area of approximately 3 km^2 and is lower-lying than Inaccessible Island, the highest peak being approximately 370 m (Wace & Holdgate 1976). There are no permanent streams on Nightingale, but there are three bogs (The Ponds) in the central part of the island (Figure 3).

The climate of Inaccessible and Nightingale Islands is cool temperate oceanic (Wace & Holdgate 1976). There are few meteorological observations from the islands, but

* National Botanical Institute, Compton Herbarium, Private Bag X7, Claremont 7735.
** Percy FitzPatrick Institute for African Ornithology, University of Cape Town, Rondebosch 7700.
*** Botany Department, University of Cape Town, Rondebosch 7700.
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FIGURE 1. —A view of Inaccessible Island from the north. The island is characterised by its steep cliffs.

FIGURE 2.—Map of Inaccessible Island showing the major collecting sites. (Adapted from Fraser *et al.* 1983.).

FIGURE 3.—Map of Nightingale Island showing the major collecting sites. (Adapted from Groves 1981).

the climate near sea level is probably similar to that recorded at Tristan da Cunha, 40 km away (see Wace & Holdgate 1976). Mean daily minimum and maximum temperatures measured during October 1989 and December to March 1989–90 at Blenden Hall, ± 10 m above sea level at Inaccessible Island, were 14.0°C and 21.6°C (range 7.5–28°C). Temperatures on the plateau are considerably cooler than those at the coast. Relative humidity at Blenden Hall varied between 52% and 100% (mean 82.5%). The prevailing winds are from the west, and there is often a marked altitudinal variation in wind strength; winds are stronger on the plateau than along the coast.

Rain is typically associated with the passage of frontal systems and occurs throughout the year, with a winter maximum (Wace & Holdgate 1976). The mean rainfall at Blenden Hall, Inaccessible Island was 151 mm per month during summer, with at least some rain on 73% of days. Rainfall on the plateau was approximately one-third higher than that recorded near sea level, and precipitation on the plateau is higher still due to the frequent formation of orographic clouds (typically above 350m). Orographic cloud covered the top of Inaccessible Island on 50.4% of days during summer 1989–90. Nightingale Island, 22 km distant from Inaccessible Island, presumably has a similar climate to that at Inaccessible. However, being a lower island, Nightingale has less marked altitudinal variation in climate, and has orographic cloud cover less frequently than does Inaccessible Island.

VEGETATION

The origin of the floras of isolated, geologically young islands by means of long distance dispersal has been discussed extensively (e.g. Tryon 1966; Carlquist 1980; Huntley 1967; Wace 1960). The main dispersal vectors of propagules to the Tristan islands are transport by wind, birds and ocean currents (Wace & Dickson 1965). The origin of the Tristan flora is primarily South American or southern circumpolar (Wace & Dickson 1965; Tryon 1966). Preece *et al.* (1986) discuss the Quaternary paleobotany of Inaccessible Island.

The vegetation types of the various islands in the Tristan group are broadly similar, and we have adopted the terminology used by Wace & Holdgate (1958) and Wace

& Dickson (1965). We recognize four physiognomically distinct types of vegetation or formations (Figures 4 & 5), which can be divided into several communities characterised by different dominant species. The communities are used as a unit of description and can be grouped in their formations as follows: 1, tussock grassland: *Spartina arundinacea* tussock; *Blechnum penna-marina* heath. 2, fern bush: *Blechnum palmiforme* heath; *Phylica arborea* bush. 3, wet heath. 4, bogs: *Sphagnum* bog; *Scirpus sulcatus* bog.

Tussock grassland

Tussock grassland covers most of Nightingale Island and occurs along the steep cliffs from sea level to ± 500 m on Inaccessible Island. The formation consists of large *Spartina arundinacea* tussocks which are up to 3.5 m tall. On drier, more exposed ridges *S. arundinacea* tussock is replaced by *Blechnum penna-marina* heath on the west coast of Inaccessible Island.

Spartina arundinacea tussock

On Inaccessible Island this community forms extensive stands on the small areas of flat ground at sea level and on all the steep sea-facing cliffs up to ± 500 m (Figure 6). It penetrates the plateau only in the low-lying river valleys above the Waterfall and Cave Rock. In areas of tall, dense growth, the closely spaced tussocks exclude all other vascular plants.

On drier, better drained ridges and in marshy areas the tussocks are more widely spaced, allowing multi-species communities to form. The species more commonly found on ridges and slopes include *Blechnum australe, B. penna-marina, Elaphoglossum laurifolium, E. succisifolium, Rumohra adiantiformis, Empetrum rubrum* and *Nertera depressa*. In marshy areas *Amauropelta bergiana* var. *tristanensis, Carex insularis, Mariscus congestus, Holcus*

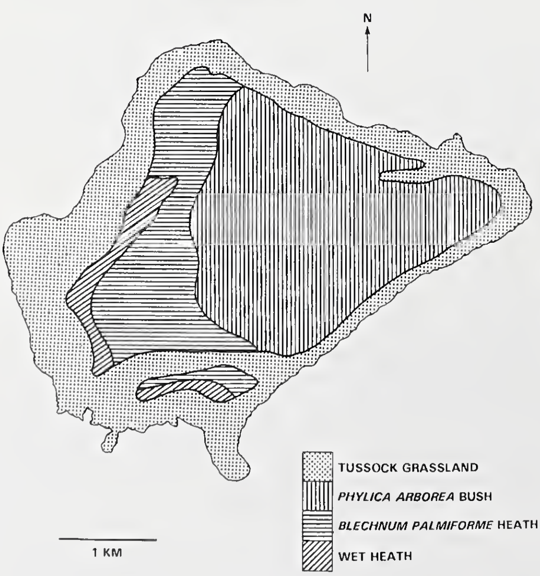

FIGURE 4.—Map of Inaccessible Island showing the distribution of the major vegetation types.

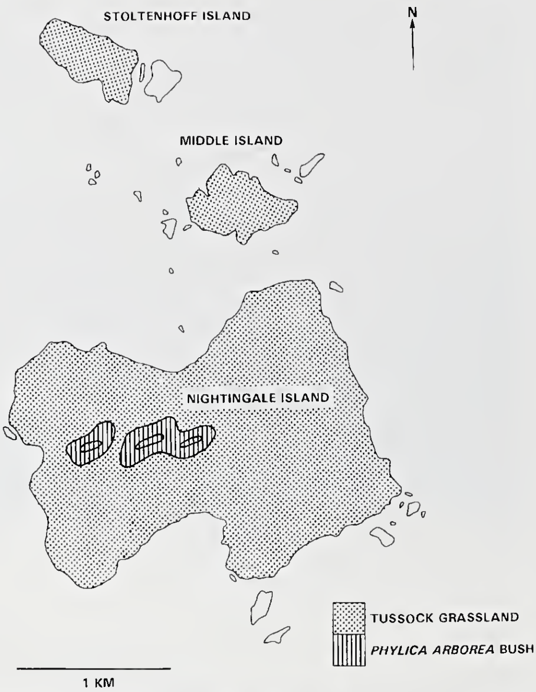

FIGURE 5.—Map of Nightingale Island showing the distribution of the major vegetation types.

lanatus, Hydrocotyle capitata, Rumex frutescens and *Scirpus sulcatus* var. *sulcatus* are commonly found. *Calystegia sepium* subsp. *americana* and *C. tuguriorum* climb over *Spartina* tussock in some areas.

Small streams and seepages run down the steep slopes onto the boulder beaches with *Azolla filiculoides, Plantago major* and *Rumex obtusifolius* subsp. *obtusifolius* commonly occurring on the streambanks. *Apium australe* and *Sonchus oleraceus* are common on the eroded talus slopes above the beach between Dirleton Point and Warren's Cliff. Rockhopper penguins (*Eudyptes chrysocome*) erode paths in their colonies under the tussock, resulting in some tussocks standing on a root pillar up to 300 mm high.

Soil slips are common on the steep coastal scarps and alien species are among the first plants to become established. Introduced species recorded on slips on Inaccessible Island include *Conyza albida, Holcus lanatus, Pseudognaphalium luteo-album, Plantago major, Sonchus oleraceus* and *Veronica serpyllifolia*, whereas *Apium australe, Pelargonium grossularioides, Scirpus bicolor* var. *virens* and various mosses are native species that colonize slips.

On Nightingale Island *Spartina arundinacea* tussock extends over most of the island. The tussock bases are more widely spaced, with the open areas between tussocks extensively burrowed into by great shearwaters (*Puffinus gravis*) for nests. Species more commonly found among the tussock include *Hypolepis rugosula* var. *villoso-viscida, Histiopteris incisa* var. *carmichaeliana* and *Scirpus bicolor* var. *bicolor*. *Asplenium obtusatum* var. *crassum* and *A. platybasis* var. *subnudum* were found less commonly.

FIGURE 6.—Tussock grassland: *Spartina arundinacea* on the low-lying plain at West Point, Inaccessible Island.

Disturbed open areas, especially along the path between the huts and the Ponds, have largely been taken over by introduced species such as *Holcus lanatus, Poa annua, Rumex obtusifolius* and *Sonchus oleraceus*. Native species found here are *Apium* sp., *Cotula australis, C. moseleyi* and *Scirpus bicolor* var. *bicolor*.

Blechnum penna-marina heath

This community is largely confined to well-drained ridges and steep slopes within tussock grassland on the west-facing coastal scarp of Inaccessible Island. *Blechnum penna-marina* generally is dominant, but species such as *Blechnum australe, Elaphoglossum succisifolium, E. laurifolium, Lycopodium diaphanum, Acaena sarmentosa, Empetrum rubrum, Holcus lanatus, Nertera depressa, Uncinia brevicaulis, Vulpia bromoides* and various mosses also occur. *S. arundinacea* and *Ctenitis aquilina* are commonly associated with boulder strewn streambeds, gullies and cliff bases. This association does not occur on Nightingale Island, where *Blechnum penna-marina* is scarce.

Fern bush

This formation covers most of the plateau on Inaccessible Island, but is restricted to the region around the Ponds at Nightingale Island. Two major associations can be identified.

Blechnum palmiforme heath

This association covers much of the high, western half of the plateau on Inaccessible Island (Figures 4 & 7). It extends from $\pm$ 250 m to the highest part of the island at Swale's Fell. Typical *Blechnum palmiforme* heath is absent from Nightingale Island, although small stands of *B. palmiforme* occur at First and Second Ponds.

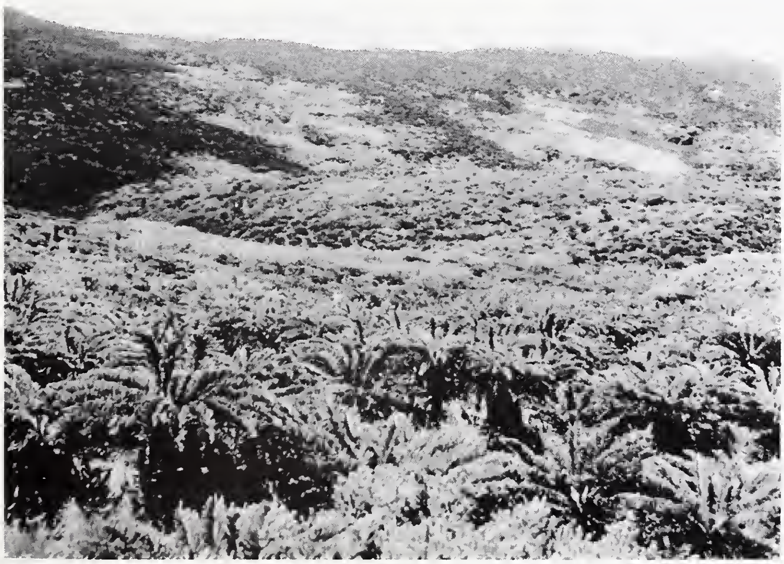

FIGURE 7.—Fern bush: *Blechnum palmiforme* heath on the plateau, Inaccessible Island. *B. palmiforme* and *Phylica arborea* are dominant in this community. The stunted growth of the plants may be ascribed to the prevailing westerly wind.

Blechnum palmiforme is the dominant species and the procumbent caudices form a confused tangle with only the apical part turning upwards, bearing a crown of coriaceous fronds 200–400 mm above the ground. Several species of these ferns (e.g. *Elaphoglossum hybridum, E. laurifolium, E. succisifolium, Grammitis magellanicum* subsp. *magellanicum, Hymenophyllum aeruginosum, H. peltatum, Lagenophora nudicaulis, Nertera assurgens* and *N. depressa*) are epiphytic on the caudices. *Eriosorus cheilanthoides, Huperzia insularis, Lycopodium diaphanum, Apium australe, Calamagrostis deschampsiiformis, Carex thouarsii, Scirpus bicolor* var. *bicolor* and *Uncinia meridensis* are frequent non-epiphytes in this association. Watercourses support a number of other taxa including *Callitriche christensenii, Glyceria insularis, Scirpus sulcatus* var. *sulcatus*, and the introduced species *Holcus lanatus* and *Rumex obtusifolius*. Stunted, procumbent *Phylica arborea* scrub occurs on some slopes and ridges. These plants never flower and usually adopt the height of the surrounding vegetation as a result of the exposed, windswept habitat.

Phylica arborea bush

This association is largely confined to the more sheltered eastern part of Inaccessible Island at elevations of ± 150–250 m. Moving from *B. palmiforme* heath, the initially procumbent *Phylica arborea* scrub becomes progressively taller, until it eventually forms a closed canopy up to 5 m high in well sheltered localitites (Figure 8). *P. arborea* branches support dense growths of epiphytic lichens and some ferns such as *Hymenophyllum aeruginosum*. The undergrowth consists largely of dense stands of pteridophytes with *Blechnum palmiforme, Ctenitis aquilina* and *Histiopteris incisa* var. *carmichaeliana* the dominant species, although *Elaphoglossum laurifolium* and *Asplenium obtusatum* var. *crassum* form monospecific stands in places. In some areas with dense canopy cover, there is little understorey vegetation, and the ground is extensively burrowed by breeding great shearwaters.

FIGURE 8.—Fern bush: *Phylica arborea* bush on the plateau, Inaccessible Island. In sheltered localities the trees may attain a hight of up to 5 m.

The Serengeti, a flat, relatively dry region in the centre of Inaccessible Island, consists of open *P. arborea* woodland. *B. palmiforme*, which attains a height of up to 2 m, forms a subcanopy between the trees. The ground storey is sparse, with *Eriosorus cheilanthoides, Carex thouarsii* var. *thouarsii, Empetrum rubrum, Nertera depressa, Scirpus bicolor* var. *bicolor* and various mosses the most abundant species. Several taxa are very scarce or absent in this area including all grasses, *Acaena sarmentosa, Ctenitis aquilina, Lagenophora nudicaulis* and *Gnaphalium thouarsii*.

Phylica arborea trees also occur in tussock grassland on the coastal slopes of Inaccessible Island, and are absent only between Dirleton Point and South Hill. Trees occur singly, in small groups, and occasionally in larger groups with closed canopies (such as Wilkins' Copse, east of Skua Bog at the West Point of Inaccessible Island). These trees differ markedly from those on the island plateau. There are very few epiphytic lichens on the branches (presumably due to the infrequency of precipitation from mist and clouds at lower altitudes) and the understorey consists either mainly of *Spartina arundinacea* or has a composition similar to *Blechnum penna-marina* heath.

On Nightingale Island, closed-canopy *Phylica arborea* bush is confined to the vicinity of The Ponds. In damp areas the undergrowth consists largely of *Blechnum palmiforme* and *Scirpus bicolor* var. *bicolor*, but the drier slopes support *Ctenitis aquilina, Hypolepis rugosula* var. *villoso-viscida, Histiopteris incisa* var. *carmichaeliana, Carex thouarsii* var. *thouarsii* and *Acaena sarmentosa*. Scattered *P. arborea* also occurs in tussock grassland, particularly along drainage lines on the eastern peak. In open areas around the Ponds, *Scirpus bicolor* var. *bicolor* forms dominant stands or hummocky meadows. Each tussock has a pachycaul habit.

Wet heath

Wet heath is restricted to the highest part of Inaccessible Island, in a narrow strip along the western edge of the plateau. It is absent from Nightingale Island. Occurring on the highest part of Inaccessible Island, it is exposed to very strong winds, and the vegetation is dense and low-growing (typically 200–300 mm). The formation is geographically limited, and could be considered to be a transitional form between tussock grassland and *B. palmiforme* heath. However, it has several characteristic species, and the large number of breeding birds concentrated in this vegetation type result in a very different proportional composition of the vegetation.

The main community extends along the western rim of the plateau between Swale's Fell and the upper part of Ringeye Valley. This is a diverse community, and the following species are common: *Amauropelta bergiana* var. *tristanensis, Ctenitis aquilina, Elaphoglossum succisifolium, Hypolepis rugosula* var. *villoso-viscida, Acaena sarmentosa, Apium australe, Carex insularis, C. thouarsii* var. *thouarsii, Holcus lanatus, Hydrocotyle capitata, Nertera assurgens, Scirpus bicolor* var. *bicolor, S. sulcatus* var. *sulcatus, Spartina arundinacea, Uncinia brevicaulis* and *U. meridensis*. This is the only area where *Glyceria insularis* is found away from watercourses, and *Cardamine glacialis, Deschampsia mejlandii* and *Ranunculus mauricatus* occur nowhere else on Inaccessible Island. Disturbed areas in the immediate vicinity of albatross nests and petrel burrows are colonised by invasive species such as the introduced *Cerastium fontanum, Holcus lanatus, Poa annua* and *Rumex obtusifolius*, as well as native species such as *Gnaphalium thouarsii*.

Southeast of Swale's Fell and in the northern part of Ringeye Valley, typical wet heath is absent, and tussock grassland merges almost directly into *Blechnum palmiforme* heath. However, there is a peculiar mixture of the two formations at Dune Hills, with sparse *Spartina arundinacea* growing in amongst *B. palmiforme* heath. Farther northwest, towards Molly Bog, *S. arundinacea* is replaced by abundant tussocks of *Calamagrostis deschampsiiformis*.

Exposed rocks and cliffs provide a microhabitat utilised by several species. Species characteristic of damp, shaded crevices include *Asplenium erectum, Elaphoglossum obtusatum, Grammitis magellanica* subsp. *magellanica, Agrostis* sp., *Lagenophora nudicaulis, Nertera depressa* and *Uncinia compacta*, whereas sunny, north and west-facing cliffs support species such as *Asplenium obtusatum* var. *crassum* and *Chenopodium ambrosioides* var. *tomentosum*.

Bogs

We consider bogs as vegetated areas with impeded drainage. Two bogs with differing vegetation types are recognised.

Sphagnum bog

There are several relatively small bogs dominated by the moss *Sphagnum* sp. on the eastern part of the plateau on Inaccessible Island. Most are located at the head of small streams. Dick's Bog in Ringeye Valley has been described in detail by Preece *et al.* (1986). Associated species are *Histiopteris incisa* var. *carmichaeliana, Carex insularis, C. thouarsii, Scirpus sulcatus* var. *sulcatus* and *Spartina arundinacea*. This type of bog is not found on Nightingale Island.

Scirpus sulcatus bog

Skua Bog, at West Point, Inaccessible Island, is an extensive marshy area at approximately sea level, dominated by *Scirpus sulcatus* var. *sulcatus* with a small area of open water along the coastal edge (Preece *et al.* 1986) (Figure 9). *Azolla filiculoides, Carex insularis, Holcus lanatus* and *Rumex frutescens* are the only other species growing in the bog, which is surrounded by tussock grassland. A smaller patch of bog occurs behind the beach to the west of Blenden Hall, which is invaded by the alien species *Mariscus congestus* and *Plantago major*.

Small patches of *Scirpus sulcatus* bog are also found in watercourses on the plateau at Inaccessible Island (e.g. Molly Bog). These bogs are often invaded by *Holcus lanatus*, and may support some *Carex insularis* and *C. thouarsii* var. *thouarsii*. Many bogs on the plateau are associated with breeding white-chinned petrels (*Procellaria aequinoctialis conspicillata*). This species only breeds in wet areas on the plateau of Inaccessible Island, and their burrows are characterised by entrance moats. The mud and water around the burrow entrance support *Hypolepis rugosula* var. *villoso-viscida, Callitriche christensenii* and *Scirpus bicolor* var. *bicolor*. In some areas, large numbers of white-chinned petrels breed together at the upslope edge of a bog, and there is a specific pattern of bog colonization. Immediately in front of the nests is an area of open water and bare mud, and at some distance from the focus of bird disturbance this is colonized by

FIGURE 9.—Bogs: *Scirpus sulcatus* bog. Skua Bog at West Point, Inaccessible Island, dominated by *Scirpus sulcatus* var. *sulcatus*.

FIGURE 10.—First Pond, Nightingale Island. Vegetation in this bog consists of an outer zone dominated by *Scirpus sulcatus* var. *sulcatus* followed by a zone of *Blechnum palmiforme*. The central part of the bog is dominated by *Phylica arborea*. The nesting bird is a yellow-nosed albatross, *Diomedea chlororhynchos*.

Callitriche christensenii. Still farther from the nests, there is the usual stand of *Scirpus sulcatus* var. *sulcatus*.

The Ponds on Nightingale Island also support floating mats of *Scirpus sulcatus* var. *sulcatus*, with little open water (Figure 10). *Carex insularis* and *C. thouarsii* also occur, and *Callitriche christensenii* is found in the shallow water along the edge of The Ponds.

DISCUSSION AND CONCLUSIONS

Seven species and one variety were recorded new from Inaccessible Island, whereas two species were found to be new for Nightingale Island. These figures exclude two taxa that may prove to be new species (*Apium* sp. and *Elaphoglossum* sp.). Our observations bring the total number of species recorded from the islands to 98 and 43 for Inaccessible and Nightingale, respectively (Table 1). Only three taxa are found on Nightingale that are absent from Inaccessible, the two species of *Cotula* (one endemic and one introduced) and the endemic *Atriplex plebeja*. A total of 28 introduced vascular plants occur on the islands, all spermatophytes. The proportion of alien plants is greater on Inaccessible Island (27.7%) than on Nightingale Island (16.3%).

TABLE 1.—Numbers of species of vascular plants on Inaccessible and Nightingale Islands. Endemic species are those entirely restricted to the Tristan-Gough group of islands, and does not include endemic varieties or subspecies

	Number of species			
	Endemic	Native	Alien	Total
Inaccessible Island				
Pteridophytes	12	16	0	28
Gymnospermae	0	0	1	1
Dicotyledons	6	15	16*	37*
Monocotyledons	14	6	9	29
Total	31	37	26*	94*
Nightingale Island				
Pteridophytes	7	11	0	18
Gymnospermae	0	0	0	0
Dicotyledons	5	6	4	15
Monocotyledons	4	3	3	10
Total	16	20	7	43
Both islands combined	34	37	27	98

* includes two species which may be extinct (*Raphanus sativus* and *Physalis peruviana*), but excludes *Centella asiatica*, for which there is no collected material.

The current survey increased the known species richness at the two islands by almost 10% (cf. Groves 1981). Only one new taxon was an introduced species (*Conyza albida* on Inaccessible Island), suggesting that the rate of transfer from the adjacent inhabited island of Tristan is relatively low. Tristan has more than 100 introduced species (Groves 1981). The low proportion of new introduced species also indicates that further collecting of the native flora is warranted, and that the number of vascular plants probably is larger than that reported here. Some taxa require systematic review, notably *Nertera*, *Uncinia*, some of the grasses (*Agrostis*, *Calamagrostis* and *Deschampsia*), and some of the ferns (*Elaphoglossum* and *Asplenium*).

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SPECIES ACCOUNT

The following accounts briefly describe the status, distribution and ecology of the vascular plants recorded from Inaccessible and Nightingale Islands. All comments refer to Inaccessible Island, unless otherwise stated. Alien species are marked with asterisks, unrecorded, incorrect species/names with a dagger and the distribution within the Tristan/Gough Islands is denoted by the initial letters of island names (G = Gough, I = Inaccessible, N = Nightingale, and T = Tristan). Author abbreviations follow Stafleu & Cowan (1976–1988). The taxa are arranged alphabetically.

PTERIDOPHYTA

ADIANTACEAE
Adiantoideae

Adiantum poiretii Wikstr.: 443 (1825).

Rare at Inaccessible Island, where it was found at only one site, growing as a lithophyte on exposed north-facing cliffs at an elevation of ± 300 m.

Distribution: G, I, N, T. *Roux 2094, 2184* (NBG).

Eriosorus cheilanthoides (Swartz) A.F. Tryon: 271 (1966).

Grammitis cheilanthoides Swartz: 23, 219 (1806).

Fairly abundant on the upper slopes and plateau, chiefly above 250 m. It occurs primarily in fairly sheltered microhabitats in fern bush and wet heath. It is particularly abundant between decumbent *Blechnum palmiforme* caudices and in moss beds among *Phylica* scrub.

Distribution: G, I, T. *Dean 832* (BOL); *Roux 2122, 2137, 2162, 2218* (NBG).

Vittaria vittarioides (Thouars) C. Chr.: 655 (1905).

Pteris vittarioides Thouars: 31 (1808).

Common above 200 m on the plateau and upper slopes of Inaccessible Island. It is widespread in wet heath and *B. palmiforme* heath, and is locally common in *Phylica* woodland, but is absent from the Serengeti. It also occurs in exposed conditions as a lithophyte on rock outcrops or low cliffs. In deeply shaded and sheltered conditions the fronds may be pendulous, whereas in exposed habitats they are erect.

Distribution: endemic, G, I, N, T. *Dean 817, 858* (BOL); *Roux 2117, 2139, 2161, 2172, 2192, 2200* (NBG).

ASPLENIACEAE
Asplenioideae

Asplenium alvarazense R.N.R. Brown: 247 (1905).

Uncommon, distributed sparsely above 300 m on moist soil slopes shaded by dense stands of *Ctenitis aquilina*.

Distribution: endemic, G, I, T. *Roux 2157, 2163* (NBG).

A. erectum Bory ex Willd.: 328 (1810).

Fairly common at all altitudes, growing on shaded rocks or under other vegetation including *Spartina* tussock and fern communities, but is never dominant.

Distribution: G, I, N, T. *Dean 828* (BOL); *Roux 2096, 2158, 2178, 2191, 2211* (NBG).

A. obtusatum G. Forster var. **crassum** (Thouars) C. Chr.: 12 (1937).

A. crassum Thouars: 33 (1808).

Common at all altitudes, frequently growing on exposed cliffs. Also occurs on flat ground, in moist conditions among boulders near sea level, but is more widespread on the plateau. In *Phylica* woodland plants form clusters up to 1.2 m in diameter. It is apparently fairly resistant to trampling, occurring with *Scirpus bicolor* at albatross loafing sites.

Distribution: endemic var., G, I, N, T. *Dean 777* (BOL); *Roux 2054, 2107, 2125, 2141, 2154, 2177, 2194, 2204* (NBG).

A. platybasis Kunze ex Mett. var. **subnudum** C. Chr.: 15 (1940).

Fairly common above 250 m, generally in exposed conditions among grasses and sedges in wet heath, but also under *Phylica* woodland. It was found among *Spartina* tussocks on Nightingale Island for the first time.

Distribution: endemic var., I, N. *Dean 831* (BOL); *Roux 2108, 2142, 2150, 2160, 2174, 2199* (NBG).

Athyrioideae

Athyrium medium (Carm.) Moore: 186 (1857).

Aspidium medium Carm.: 511 (1818).

Fairly common on the plateau, primarily above 200 m, but down to 100 m along the river above Waterfall Beach. It grows in wet, fairly sheltered conditions on streambanks, cliffs and amongst other ferns in fern bush and wet heath vegetation.

Distribution: endemic, I, T. *Roux 2119, 2155* (NBG); *Ryan 127* (NBG).

Dryopteridoideae

Ctenitis aquilina (Thouars) Pic. Serm.: 468 (1973).

Polypodium aquilinum Thouars: 32 (1808).

It occurs at all altitudes, but at lower elevations it is largely restricted to watercourses and boulder fields at the base of cliffs. Abundant over much of the plateau, where plants are stunted in wet heath and *Blechnum palmiforme* heath compared to those at lower altitudes. It often forms extensive dominant stands under *Phylica* woodland, but is absent from the Serengeti.

Distribution: endemic, G, I, N, T. *Dean 810* (BOL); *Roux 2092, 2147, 2193* (NBG).

Elaphoglossoideae

Elaphoglossum campylolepium J.P. Roux: 234 (1991).

The species is evidently restricted to higher elevations and on Inaccessible Island it is known from ± 450 m. It often grows in association with *E. succisifolium* in exposed or sheltered conditions.

Distribution: endemic, I, T. *Roux 2114, 2132* (NBG).

E. hybridum (Bory) Brack.: 69 (1854).

Acrostichum hybridum Bory: 95 (1811).

Fairly common in fern bush above 200 m, growing primarily on *Blechnum palmiforme* caudices, but also on cliffs and rock overhangs.

Distribution: G, I, T. *Dean 835* (BOL); *Roux 2099, 2105, 2140, 2146, 2148* (NBG).

E. laurifolium (Thouars) Moore: 14 (1857).

Acrostichum laurifolium Thouars: 31 (1808).

Like *E. succisifolium*, this species is common at all altitudes and is present in all vegetation types. It prefers more sheltered habitats than *E. succisifolium*. It often forms dense monospecific stands in *Phylica* woodland with fronds attaining a length of 400 mm.

An apparently undescribed *Elaphoglossum* species occurs on Inaccessible Island. It is distinguished from *E. laurifolium* by its narrower, less robust fronds, the somewhat elevated midrib on the adaxial surface, and the stellate scales on the abaxial surface. It is patchily distributed on the plateau between 200–400 m, where it forms large dominant stands on exposed ridges and streambanks. Few fertile fronds were found throughout the summer.

Distribution: endemic, G, I, N, T. *Dean 801, 875* (BOL); *Roux 2072, 2090, 2144, 2179, 2195, 2205* (NBG).

E. obtusatum (Carm.) C. Chr.: 20 (1940).

Acrostichum obtusatum Carm.: 510 (1818).

Scarce, restricted to the western plateau and upper slopes above 350 m, where it grows in overhangs and on shaded boulders and cliffs.

Distribution: endemic, I, T. *Roux 2107, 2125, 2154* (NBG).

E. succisifolium (Thouars) Moore: 15 (1857).

Acrostichum succisifolium Thouars: 31 (1808). (as *succisaefolium*).

Abundant at all altitudes and present in all vegetation types. It occurs as a geophyte in deep moss in gullies, on exposed cliffs and rocks and as an epiphyte on caudices of *Blechnum palmiforme*.

Distribution: endemic, G, I, N, T. *Dean 800* (BOL); *Roux 2069, 2073, 2143, 2164, 2196, 2206* (NBG).

AZOLLACEAE

Azolla filiculoides Lam.: 343 (1783).

Common on floating *Scirpus sulcatus* in Skua Bog, and also occurs in two smaller bogs towards Blenden Hall. Elsewhere it is restricted to permanent seepages on cliffs and slips above the beach between Dirleton Point and North Point.

Distribution: I. *Dean 776* (BOL); *Roux 2058, 2065* (NBG).

BLECHNACEAE

Blechnum australe L.: 130 (1767).

Virtually restricted to the coastal slopes, where it occurs sporadically up to 350 m, although mostly below 200 m. It is scarce in the valley above the Waterfall. It is common in slightly shaded areas among *Spartina* tussocks and in association with *Blechnum penna-marina*. It also grows in more exposed conditions in crevices among boulders, and occasionally on cliffs. *B. australe* was collected for the first time at Nightingale Island.

Distribution: G, I, N, T. *Dean 798* (BOL); *Roux 2059, 2185, 2190* (NBG).

B. palmiforme (Thouars) C. Chr.: 10 (1940).

Pteris palmiformis Thouars: 30 (1808).

Occurs at all altitudes, and is the dominant plant on much of the plateau. On the high western plateau the caudices are procumbent, forming a confused tangle (evocatively described by Carmichael 1818), whereas in *Phylica* woodland, where the plants are more protected, the caudices may reach a height of up to 2 m. The species is scarce on the coastal slopes, occurring in small numbers on ridges.

Distribution: endemic, G, I, N, T. *Roux 2070, 2111, 2189* (NBG).

B. penna-marina (Poir.) Kuhn: 92 (1868).

Polypodium penna-marina Poir.: 520 (1811).

Common at all altitudes, often forming extensive dominant stands on exposed ridges on the coastal slopes in the west. It is seldom dominant on the plateau, but is widespread, occurring at low densities in all vegetation types. Juvenile fronds are reddish, and fertile fronds are produced in summer.

Distribution: G, I, N, T. *Dean 802* (BOL); *Roux 2066, 2074, 2145, 2186* (NBG).

DAVALLIACEAE
Davallioideae

Rumohra adiantiformis (G. Forster) Ching: 70 (1934).

Polypodium adiantiforme G. Forster: 14 (1786).

Restricted to the coastal slopes, mostly below 250 m, although a small population was found on the slump below the northwest-facing scarp at ± 400 m. It is common in tussock grassland, primarily in *Blechnum penna-marina* heath, often forming large stands on steep slopes and ridges. It is scarce on the northeast coast, only found at the huts near the Waterfall.

Distribution: G, I, T. *Dean 772, 799* (BOL); *Roux 2056, 2169, 2182* (NBG).

DENNSTAEDTIACEAE
Dennstaedtioideae

Histiopteris incisa (Thunb.) J. Sm. var. **carmichaeliana** (Agardh) C. Chr.: 15 (1937).

Pteris vespertilionis (Labill.) J. Sm. var. *carmichaeliana* Agardh: 80 (1839).

Occurs at all altitudes in moist conditions. At low elevations it is restricted to deep shade among *Spartina* tussocks, whereas on the plateau it is more widespread. It is abundant in fern bush, forming dense monospecific stands in some areas (e.g. Harold's Plain), but is scarce in wet heath. The plants are deciduous.

Distribution: endemic var., G, I, N, T. *Dean 808* (BOL); *Roux 2103, 2167, 2188* (NBG).

Hypolepis rugosula (Labill.) J. Sm. var. **villoso-viscida** (Thouars) C. Chr.: 15 (1937).

Polypodium villoso-viscidum Thouars: 33 (1808).

Occurs primarily above 200 m, on the plateau and upper slopes of Inaccessible Island, but also down to sea level at Waterfall Beach. It generally grows in association with breeding birds, and is common in disturbed areas in wet heath. It is absent from the Serengeti where burrow-nesting birds are scarce. On the western scarp it occurs along streambeds under *Spartina* down to 300 m.

Distribution: endemic var., G, I, N, T. *Roux 2091, 2120, 2166, 2187* (NBG).

GRAMMITIDACEAE

Grammitis magellanica Desv. subsp. **magellanica**.

Fairly common on the plateau above 200 m, growing as an epiphyte on caudices of *Blechnum palmiforme* and, less frequently, on moist, shaded cliffs. All the *Grammitis* collections made during the expedition conform with the diagnostic features of *G. magellanica* var. *magellanica* provided by Parris (1981). It therefore appears as if *G. poeppigiana* (Parris 1981), which has previously been reported from Inaccessible, is incorrect.

Distribution: G, I, N, T. *Dean 837* (BOL); *Roux 2126, 2127, 2128, 2152, 2153, 2156, 2165* (NBG).

HYMENOPHYLLACEAE

Hymenophyllum aeruginosum (Poir.) Carm.: 518 (1818).

Trichomanes aeruginosum Poir.: 76 (1808).

A common epiphyte or lithophyte in moist, shaded localities above 200 m. It is particularly abundant on caudices of *Blechnum palmiforme* in sheltered locations.

Distribution: endemic, G, I, N, T. *Dean 836* (BOL); *Roux 2095, 2118, 2135, 2215, 2216* (NBG).

H. peltatum (Poir.) Desv.: 333 (1827).

Trichomanes peltatum Poir.: 76 (1808).

Occurs in similar habitats to *H. aeruginosum*, at elevations above 350 m, but appears to prefer the most shaded, moist sites. It is less abundant than *H. aeruginosum*.

Distribution: G, I, T. *Roux 2136, 2173* (NBG).

†**Trichomanes angustatum** Carm.: 513 (1818).

Previously recorded from shaded, wet rocks under *Spartina arundinacea* (Groves 1981). It was not recorded during the current survey.

Distribution: I, N, T.

LYCOPODIACEAE

Huperzia insularis (Carm.) Roth.: 60 (1944).

Lycopodium insulare Carm.: 509 (1818).

Fairly common at elevations exceeding ± 250 m, often in steep, exposed conditions with low vegetation cover. In *Phylica* scrub where plants are more protected they often form large clumps with stems up to 250 mm tall.

Distribution: endemic, G, I, N, T. *Dean 833* (BOL); *Roux 2124, 2138, 2159* (NBG).

Lycopodium diaphanum (Beauv.) Swartz: 180 (1806).

Lepidotis diaphana Beauv.: 108 (1805).

Common at all altitudes, in *Blechnum penna-marina* heath, fern bush and wet heath. Although more abundant on exposed ridges and slopes, it also occurs in partially shaded conditions under *Phylica* scrub. Rapidly colonizes slips on the plateau. Spores are released from mid-January to March.

Distribution: endemic, G, I, T. *Dean 805* (BOL); *Roux 2097, 2102, 2112* (NBG).

THELYPTERIDACEAE

Amauropelta bergiana (Schlecht.) Holttum var. **tristanensis** Holttum: 134 (1974).

Common at all altitudes, but below 200 m it is largely restricted to bogs among *Spartina* tussock and along watercourses. It is widespread on the plateau, but is nowhere dominant.

Distribution: endemic var., G, I, N, T. *Dean 815* (BOL); *Roux 2068, 2075, 2149* (NBG).

SPERMATOPHYTA–GYMNOSPERMAE

PINACEAE

* **Pinus caribaea** Morelet: 106, 107 (1851).

Three trees still grow behind the huts at Waterfall Beach (cf. Wace & Holdgate 1976), with no sign of seedlings despite producing cones with seeds.

Distribution: I. *Ryan 92* (BOL).

MONOCOTYLEDONES

CYPERACEAE

Carex insularis Carm.: 508 (1818).

Occurs in wetter situations than *C. thouarsii* at all altitudes. At sea level it is largely restricted to bogs such as Skua Bog, and on the plateau occurs along watercourses. It is, however, more widespread in wet heath. Distinguished from *C. thouarsii* by its triangular (cf. terete) culm and drooping (cf. erect) spike.

Distribution: endemic, G, I, N, T. *Dean 804, 860* (BOL); *Roux 2067, 2202* (NBG); *Ryan 108* (BOL).

C. thouarsii Carm.: 508 (1818).

var. **recurvata** Christoph.: 1 (1944).

Widespread in open habitats such as soil slips and around albatross nests. It is distinguished from *C. thouarsii* var. *thouarsii* by its smaller size, which may merely be a consequence of growing in drier habitats.

Distribution: endemic, G, I, T. *Dean 788* (BOL, NBG).

var. **thouarsii**

Widespread. Occurs in *Phylica* woodland at both Inaccessible and Nightingale, but is most abundant in wet heath on the plateau at Inaccessible. Many of the seed heads are completely denuded by endemic buntings.

Distribution: endemic, G, I, N, T. *Dean 787, 861* (BOL); *Roux 2203* (NBG), *Ryan 58* (BOL).

* **Mariscus congestus** (Vahl) C.B. Clarke: 72 (1897).

Cyperus congestus Vahl: 350 (1805).

Dominant in marshy areas at Blenden Hall, although not yet found at Skua Bog. It has reached the bottom of the rope on West Road at ± 100 m. It also occurs on wet slips above the beach towards Warren's Cliff, at Salt Beach (one plant), and around the huts at Waterfall Beach. Flowers December–February. Seeds are eaten by the endemic buntings, and this may facilitate dispersal because seeds sometimes are found adhering to feathers around the base of the bill.

Distribution: I, T. *Ryan 63* (BOL).

Scirpus bicolor (Carm.) Spreng.: 28 (1827).

Isolepis bicolor Carm.: 503 (1818).

var. **bicolor**

An extremely variable species, occurring throughout the islands. Two forms are found on the plateau; one tussock form with very fine leaves and small flower heads that is almost invariably associated with bird-disturbed areas, and one that forms large trailing, tangled mats, characterized by short, broad leaves and few, small-flowered heads. The latter type is particularly abundant in wet heath. At Nightingale a tussock form occurs in dominant stands, forming hummocked meadows.

Distribution: endemic, G, I, N, T. *Dean 795, 807, 820, 825, 859, 868, 871* (BOL); *Roux 2064* (NBG); *Ryan 66* (BOL).

var. **virens** (Boeck.) Hemsl.: 158 (1884).

Scirpus virens Boeck.: 261 (1875).

Forms low tussocks in rocky areas and soil slips in *Spartina arundinacea* tussock vegetation, and also forms fairly robust tussocks on the plateau. The former is common on bare ground above the beach, whereas the latter is widespread in undisturbed vegetation on the plateau. This variety has seeds twice the mass of those of var. *bicolor.*

Distribution: endemic, G, I, N, T. *Dean 794, 857* (BOL, NBG); *Ryan 65, 74* (BOL).

S. sulcatus Thouars: 36 (1808).

var. **moseleyanus** (Boeck.) Hemsl.: 155 (1884).

Scirpus moseleyanus Boeck.: 262 (1875).

Distribution: endemic var., G, I, N, T.

var. **sulcatus**

Common at all elevations in open areas, along streams, and in bogs where it forms extensive monospecific stands. Seeds germinate while in the seed head. Flowers earlier at sea level; sprouting seeds were found from December at Skua Bog, but seeds only ripened on the plateau in February–March.

Distribution: endemic var., G, I, N, T. *Dean 775, 789, 806, 821, 826, 863* (BOL); *Roux 2051* (NBG); *Ryan 91* (BOL).

Uncinia brevicaulis Thouars var. **brevicaulis**

Occurs at all altitudes, common in wet heath and widespread in fern bush on the plateau, but restricted to shaded sites near sea level, under *Spartina* tussock, *Phylica* and apple trees. Plants are smaller at low altitudes, with smaller numbers of seeds per spike and narrower leaves and seed spikes. Seeds collected near sea level average only half the mass of those from the plateau. The seeds were found attached to the plumage of a wide variety of birds. Flowers October–December, with seeds from December–February.

Distribution: endemic var., G, I, N, T. *Dean 811* (BOL); *Ryan 57, 104, 109* (BOL).

U. compacta R. Br. var. **elongata** C.B. Clarke: 395 (1883).

Restricted to the plateau, where it grows in shaded situations in *Phylica* woodland and other dense vegetation. Dwarf plants were also found growing on moss-covered boulders along the western edge of the plateau. Flowers at the same time or slightly later than *U. brevicaulis*.

Distribution: endemic var., G, I, T. *Ryan 118* (BOL).

U. meridensis Steyerm.: 61 (1951).

First record for Inaccessible, where it is common on the plateau and upper slopes above 200 m, growing in open areas in wet heath and fern bush. Unlike other species of *Uncinia*, it often forms dense stands up to 5 m in diameter. Flowers slightly earlier than *U. brevicaulis*.

Distribution: G, I, T. *Dean 849* (NBG); *Ryan 52* (BOL).

LILIACEAE

* **Phormium tenax** J.R. & G. Forster: 48, t. 24 (1776).

Introduced to Waterfall Beach area, it was reportedly grazed out by cattle (Wace & Holdgate 1976). However, Wace & Ollier (1984) noted it to be well established on the northern cliffs of Inaccessible in 1976. We found ± 20 plants, many flowering, growing halfway up the cliffs above the huts at Waterfall Beach. None were found at the huts, and only one plant (not in flower) was found on the plateau. A control programme similar to that operating at Nightingale should be instigated to eradicate this aggressively invasive species.

A few plants were found along the edge of First Pond and in *Phylica arborea* woodland at Nightingale, but these were all fairly small non-flowering plants and the ongoing control programme appears to be successful.

Distribution: I, N, T. *Dean 866* (BOL); *Roux 2210* (NBG).

POACEAE

†**Agrostis carmichaelii** J.A. Schultes & J.H. Schultes: 571 (1827).

Previously collected from Inaccessible (Groves 1981), none was identified during the current survey.

Distribution: endemic, I, T.

* **A. gigantea** Roth: 31 (1788).

Collected from the huts at Waterfall Beach (Groves 1981). Two unidentified grasses lacking reproductive organs were collected at this site on 16 February 1990 [*Ryan 97, 100* (BOL)].

Distribution: I, T.

A. goughensis C.E. Hubb.: 383 (1981).

First record for Inaccessible and the Tristan group *sensu stricto*. Fairly common along watercourses on the northern and eastern plateau; not seen away from streams. Flowers January–February.

Distribution: endemic, G, I. *Ryan 79, 114, 116* (BOL).

A. holgateana C.E. Hubb.: 383 (1981).

First record for Inaccessible. Fairly common on the plateau and upper slopes, where it forms tussocks up to 200 mm high or cushions up to 100 mm high.

Distribution: endemic, I, T. *Ryan 76, 105, 124* (BOL).

A. magellanica Lam. subsp. **laeviuscula** C.E. Hubb.: 381 (1981).

A large, robust grass restricted to watercourses on the lower, eastern plateau. Flowers January–March.

Distribution: endemic subsp., G, I, T. *Ryan 115* (BOL).

A. media Carm.: 504 (1818).

Fairly common on the plateau and upper slopes above 250 m, where it forms small, dense cushions in exposed areas. It is often found on steep slopes, such as banks and low cliffs.

Distribution: endemic, G, I, T. *Ryan 59, 67, 68* (BOL).

* **A. stolonifera** L. subsp. **stolonifera.**

Collected from the huts at Waterfall Beach (Groves 1981). Two unidentified grasses lacking reproductive organs were collected at this site on 16 February 1990 [*Ryan 97, 100* (BOL)].

Distribution: G, I, T.

†**A. trachylaena** C.E. Hubb.: 383 (1981).

Previously collected from Inaccessible (Groves 1981), none was identified during the current survey.

Distribution: endemic, I, N.

A. wacei C.E. Hubb.: 383 (1981).

First record for Inaccessible. Restricted to the western plateau and upper slopes, where it grows in exposed, open situations including boulders, streambanks and disused albatross nests.

Distribution: endemic, I, T. *Dean 845* (PRE); *Ryan 122* (BOL).

* **Aira caryophyllea** L.: 66 (1753).

Fairly common in disturbed sites and on rocks. Found at all altitudes, at Blenden Hall, along the West Road, the western plateau rim and at a few localitites on the central plateau.

Distribution: I, T. *Ryan 55, 70* (BOL).

Calamagrostis deschampsiiformis C.E. Hubb.: 383 (1981).

First record for Inaccessible. Common tussock-forming grass on the plateau above 300 m. Typically grows on exposed ridges in *Blechnum palmiforme* heath where tree ferns are shorter and less dense. It is co-dominant with *B. palmiforme* on the upper slopes of Dune Hills. Flowers December–February.

Distribution: endemic, G, I, T. *Ryan 75* (BOL).

* **Cynodon dactylon** (L.) Pers.: 85 (1805).

Panicum dactylon L.: 58 (1753).

A dense stand occurs around the huts and old cultivated area at Waterfall Beach, and has colonized the edge of the boulder beach. The proportion of seeds set was 1% (n = 239), possibly accounting for the lack of spread beyond this single locality.

Distribution: I, T. *Ryan 96* (BOL).

†**Deschampsia christophersenii** C.E. Hubb.: 388 (1981).

Collected at Inaccessible during the Norwegian Expedition in 1937-38, but not found during the current survey.

Distribution: endemic, I, T.

D. mejlandii C.E. Hubb.: 389 (1981).

A fairly scarce, robust grass restricted to a few sites in wet heath along the western edge of Inaccessible. Flowers January–February.

Distribution: endemic, I, T. *Ryan 88* (BOL).

Glyceria insularis C.E. Hubb.: 394 (1981).

Occurs on the plateau, extending down along watercourses to ± 150 m above the Waterfall. Only found away from watercourses in wet heath on the highest part of the island. Flowers October–December.

Distribution: endemic, G, I, T. *Dean 829* (BOL); *Ryan 113* (BOL).

* **Holcus lanatus** L.: 1048 (1753).

The second most widespread alien plant at Inaccessible, occurring at all altitudes, and in habitats ranging from mesic to boggy. It is common in disturbed sites such as slips and paths at Blenden Hall, and is widespread on the periphery of Skua Bog. It is the only alien to colonize undisturbed natural vegetation, and is found widely in *Blechnum pennamarina* heath and sparse *Spartina* tussock grassland at Blenden Hall. It also occurs on slips above the beach between Blenden Hall and Warren's Cliff, but is scarce on the northwestern coast, and found only at Waterfall Beach. *H. lanatus* forms dominant stands along much of the western edge of the plateau, but is scarce elsewhere on the plateau, primarily occurring along watercourses and in some *Scirpus sulcatus* bogs. It is common in disturbed areas at Nightingale, especially along the path from the huts to The Ponds. Flowers November—January, and the seeds are eaten extensively by buntings.

Distribution: G, I, N, T. *Dean 790, 856* (PRE); *Ryan 56* (BOL).

* **Poa annua** L.: 68 (1753).

Restricted to the western edge of the plateau, where it occurs in bird-disturbed areas. Extends down the West Road to ± 200 m. However, it is more common at Nightingale, where it occurs along the path leading between the huts and First Pond. It is also a common weed around the huts at Nightingale. Flowers October—February.

Distribution: G, I, N, T. *Dean 843, 872* (PRE); *Roux 2131, 2209* (NBG); *Ryan 102, 103, 107* (BOL).

†**Polypogon mollis** (Thouars) C.E. Hubb. & E.W. Groves: 399 (1981).

Phalaris mollis Thouars: 37 (1808).

Collected on the western plateau of Inaccessible during the Norwegian Expedition in 1937-38, it was not found during the current survey.

Distribution: endemic, I, T.

Spartina arundinacea (Thouars) Carm.: 504 (1818).

Ponceletia arundinacea Thouars: 36 (1808).

Occurs primarily on the coastal slopes, where it forms dense stands that often exclude all other vascular plants. Sparse stands occur in wet heath on the western plateau, but it is scarce in fern bush over much of the plateau, with only scattered patches at the river junction below Denstone Hill and in Round Hill. It extends up the low-lying, steep-sided river valleys above the Waterfall and southwest of Joe's Hill. Flowers October—December, with seed heads persisting until at least March. Seed heads size is related to plant size, and is greatest at sea level where plants can exceed 3 m in height. *Spartina* constitutes the dominant vegetation over most of Nightingale.

Distribution: G, I, N, T. *Dean 844, 845* (BOL).

* **Vulpia bromoides** (L.) S.F. Gray: 124 (1821).

Festuca bromoides L.: 75 (1753).

Fairly common introduced species, found at scattered localities on Inaccessible, from sea level to 400 m. It is particularly common on the slips and talus slopes adjacent to the West Road.

Distribution: I, T. *Roux 2098* (NBG); *Ryan 71, 89, 101, 106, 117, 128, 129* (BOL).

DICOTYLEDONES

APIACEAE

Apium australe Thouars: 43 (1808).

Common at all altitudes and in all the vegetation types. It is often associated with disturbed areas such as slips. On the exposed western plateau, plants are smaller, adopting the height of the surrounding vegetation, and have more robust and more finely dissected leaves than plants in sheltered sites. Flowers November—February.

A discrete form of *Apium* was found in association with *A. australe*, from which it differs in the longer and fewer leaves, the purplish petiole bases and the less strong odour when the leaves are crushed. This form grows up to 1.2 m tall in habitats where *A. australe* seldom exceeds 300 mm. It is fairly common on the plateau, principally in *Spartina* grassland between Molly Bog and Dune Hills, and at Where-the-Pig-Fell-Off, and less frequently in wet heath. Also occurs sporadically elsewhere on the plateau, such as along the river at Denstone Hill. Extends almost to sea level in *Spartina* tussock on the southwestern flank of Dune Hills. On Nightingale it occurs commonly along the path between the huts and The Ponds. Flowers from late November (Nightingale) to February.

Distribution: G, I, N, T. *Dean 771, 822* (BOL); *Roux 2055* (NBG); *Ryan 62* (BOL).

*†**Centella asiatica** (L.) Urban: 287 (1907).

Hydrocotyle asiatica L.: 234 (1753).

Reported from the huts at Waterfall Beach in 1962 (Wace & Dickson 1965), but no plants could be located (Groves 1981). We found no trace of this species, which is common at Tristan.

Hydrocotyle capitata Thouars: 43, t. 12 (1808).

Common at all altitudes, primarily in damp localities. It is most abundant in wet heath, in damp, open places amongst *Spartina* tussocks, and in bogs near sea level. Often grows amongst rank alien grasses along watercourses.

Distribution: G, I, T. *Dean 797* (BOL); *Ryan 61* (BOL).

ASTERACEAE

Chevreulia sarmentosa (Pers.) Blake: 85 (1925).

Tussilago sarmentosa Pers.: 456 (1807).

Collected from Inaccessible during the 1937-38 Norwegian Expedition (Groves 1981). Not found during the current survey.

Distribution: I, T.

* **Conyza albida** Willd. ex Spreng.: 512 (1826).

First record for Inaccessible Island. It is one of the most widespread and abundant alien plants, and is common on slips and other disturbed areas such as paths at Blenden Hall, Dirleton Point and Waterfall Beach. It also occurs along the West Road, and at several localities just below the plateau edge. However, it is rare on the plateau. Bushes can attain a height of 1.6 m in sheltered gulleys and have over 1 000 flower heads that produce copious small, plumed seeds.

Groves (1981) listed this plant as *C. sumatrensis* (Retz.) E.H. Walker. The correct name, however, appears to be *C. albida* (Guédès & Jovet 1975).

Distribution: I, T. *Dean 784* (BOL); *Roux 2078* (NBG); *Ryan 60* (BOL).

* **Cotula australis** (Sieber ex Spreng.) J.D. Hook.: 128 (1852).

Anacylus australis Sieber ex Spreng.: 497 (1826).

Only collected at Nightingale, where it grows with *C. moseleyi* in disturbed areas along the path leading between the huts and The Ponds.

Distribution: N, T. *Roux 2214* (NBG).

C. moseleyi Hemsl.: 152 (1884).

Widespread on Nightingale Island, occurring in disturbed or open habitats. It is common along the path from the huts to The Ponds and around yellow-nosed albatross nests, but also grows in shaded rock crevices on low cliffs.

Distribution: endemic, N. *Dean 865* (BOL); *Roux 2213* (NBG).

Gnaphalium thouarsii Spreng.: 473 (1826).

Widespread on the plateau, typically in disturbed or open sites such as slips, around bird colonies and the periphery of rocks. Frequently colonizes deserted albatross nests. Occurs down to ± 250 m on the western scarp, the approximate limit of frequent orographic cloud, but a few plants occur at sea level at The Waterfall. Biennial, flowering November—January, and seeds January—March.

Distribution: endemic, G, I, N, T. *Dean 819* (BOL).

Lagenophora nudicaulis (Comm. ex Lam.) Dusén: 98 (1900).

Aster nudicaulis Comm. ex Lam.: 308 (1783).

Fairly common on the plateau above 200 m, where it occurs primarily in *Blechnum palmiforme* heath. Grows on mosses and as an epiphyte on the caudices of *B. palmiforme*. Occasionally forms a continuous mat up to 1 m across.

Distribution: G, I, T. *Dean 818* (BOL); *Roux 2104* (NBG); *Ryan 77* (BOL).

* **Pseudognaphalium luteo-album** (L.) Hilliard & Burtt: 206 (1981).

Gnaphalium luteo-album L.: 851 (1753).

Fairly common, occurring on slips and along paths on the west-facing coastal slopes up to ± 350 m above sea level. It is absent from the plateau, but small pockets occur at sea level near Waterfall Beach and on a coastal slip at Joe's Hill.

Distribution: I, T. *Dean 783, 845* (BOL); *Roux 2079* (NBG).

* **Sonchus oleraceus** L.: 794 (1753).

A common weed, occurring along most of the coastline where it is abundant on slips and bare earth above the beach. It also occurs on coastal slips, and extends up to 400 m above sea level along the West Road and the adjacent slump. It is very scarce on the plateau (*contra* Preece *et al.* 1986), and grows in drier habitats than other introduced plants. Flowers October–March.

Distribution: G, I, N, T. *Dean 770* (BOL); *Roux 2050, 2077, 2212* (NBG).

BRASSICACEAE

* **Brassica rapa** L.: 666 (1753).

Approximately 30 bushes are restricted to within 10 m of the huts at Waterfall Beach. All had ripe seed pods on 16 February 1990.

Distribution: I, T. *Ryan 99* (BOL).

Cardamine glacialis (G. Forster) DC.: 264 (1821).

Sisymbrium glaciale G. Forster: 32 (1789).

Scarce in wet heath, where it was only recorded on the south slope of Swale's Fell, flowering in October.

Distribution: G, I, T. *Dean 842* (BOL).

*†**Raphanus sativus** L.: 669 (1753).

Collected at Waterfall Beach in 1937 (Groves 1981), it has not been found subsequently and has probably died out.

CALLITRICHACEAE

Callitriche christensenii Christoph.: 7 (1934).

Common in streams and marshy areas on the plateau, often in association with white-chinned petrel burrows. Occurs at sea level in some rivers (e.g. the Waterfall) and seepages (e.g. at Dirleton Point). Forms a floating mat in streams, but also grows on wet mud and on rock faces in waterfalls. Flowers from October to January.

Distribution: endemic, G, I, N, T. *Dean 830, 874* (BOL).

CARYOPHYLLACEAE

* **Cerastium fontanum** Baumg. var. **triviale** (Link) Jalas: 63 (1963).

Cerastium triviale Link: 433 (1822).

Restricted to the edge of the plateau, chiefly between Swale's Fell and Ringeye Valley, but with a few individuals on Joe's Hill. Grows on bare earth and rocks along the scarp edge, typically where the vegetation has been severely trampled by birds. However, also occurs commonly in the large stand of *Holcus lanatus* at the top of the West Road, and a few individuals occur down to 250 m on the West Road. Flowers December–January.

Distribution: G, I, T. *Ryan 72* (BOL).

CHENOPODIACEAE

†**Atriplex plebeja** Carm.: 508 (1818).

Known from the Nightingale archipelago and Tristan (Groves 1981), this species was not recorded during the current survey.

Distribution: endemic, N, T.

Chenopodium ambrosioides L. var. **tomentosum** (Thouars) Aellen: 6 (1968).

Chenopodium tomentosum Thouars: 38 (1808).

Patchily distributed along the upper slopes on the western side of Inaccessible, extending to sea level on the northeast coast at Waterfall Beach and Salt Beach, where dominant stands occur. Along the plateau edge often grows in sheltered, west-facing crevices and on rock faces. Forms a small bush up to 1.2 m high, flowering January–February.

Distribution: endemic var., G, I, N, T. *Ryan 80, 95* (BOL).

CONVOLVULACEAE

Calystegia sepium (L.) R. Br. subsp. **americana** (Sims) Brummitt: 216 (1965).

Convolvulus sepium L.: 153 (1753) var. *americanus* Sims: t. 732 (1804).

Patchily distributed up to 200 m above sea level. It is most abundant at Blenden Hall, where it occurs as a creeper on *Spartina* and on rank growth on slips. Smaller patches occur at the huts at Waterfall Beach and on the steep seaward slope between Joe's Hill and South Hill. The only place it was found on the plateau was in the river valley above Waterfall Gulch, between Round Hill and Denstone Hill. It has pubescent leaves longer than 30 mm, and large pink flowers are present November–January. No seeds were found on plants from Blenden Hall, but seeds were fairly common at Waterfall Beach.

Distribution: I, T. *Dean 773* (BOL); *Roux 2060* (NBG); *Ryan 64* (BOL).

†**C. soldanella** R. Br.: 483 (1810).

Listed erroneously as occurring on Inaccessible by Wace & Dickson (1965: 334, but not in the appendix, p. 338). There is no suitable habitat for this sand-loving species at Inaccessible or Nightingale.

C. tuguriorum (G. Forster) R. Br. ex J.D. Hook.: 183 (1852).

Convolvulus tuguriorum G. Forster: 14 (1786).

Restricted to a 50 m stretch of *Spartina* tussock behind the beach immediately north of Tern Rock, Blenden Hall. The trailing stems form a dense mat over the *Spartina*. Flowers in early December, but no seed was set (possibly due to the absence of an appropriate pollinator). The flowers are white and are smaller than those of *C. sepium*, and the leaves are less than 30 mm long and are glabrous. Groves (1981) considers this species to be probably native to Inacessible, but the restricted range suggests that it is a recent arrival. Its spread may be limited by vegetative reproduction.

Distribution: I. *Dean 796* (BOL); *Ryan 53* (BOL).

EMPETRACEAE

Empetrum rubrum Vahl ex Willd.: 713 (1806).

Common at all altitudes in open habitats. Colonizes slips, but also grows among mosses and low ferns in *Blechnum penna-marina* heath and fern bush. It also occurs in exposed situations in rock crevices. However, it is virtually absent from wet heath and heavily shaded sites. The dark red berries ripen December–March and are eaten extensively by the endemic thrushes and buntings.

Distribution: G, I, N, T. *Dean 832* (BOL); *Roux 2181* (NBG).

GERANIACEAE

Pelargonium grossularioides (L.) L'Hérit. in Aiton: 420 (1789).

Geranium grossularioides L.: 679 (1753).

Fairly common on partially revegetated soil slips and among rocks in *Spartina* tussock vegetation up to 200 m on the west side of Inaccessible. Absent from the plateau, and only a few individuals recorded from rock crevices on the scarp edge above the Waterfall. Distribution is similar to many alien plants, probably as a result of similar habitat requirements. Flowers from October to February.

Distribution: I, T. *Dean 780* (BOL); *Roux 2217* (NBG); *Ryan 54* (BOL).

OXALIDACEAE

* **Oxalis corniculata** L.: 624 (1753).

This species was spreading rapidly at Waterfall Beach in 1873 (Moseley 1892), but had disappeared by 1968 (Wace & Holdgate 1976). We found none at Salt Beach, but on 3 March 1990 several plants in flower and with ripe seed pods were found on the ridge northwest of the Waterfall at ± 200 m. Preece *et al.* (1986) reported it from Pig Beach Hill, an area not visited during this survey.

Distribution: I, T. *Ryan 125* (BOL).

PIPERACEAE

Peperomia berteroana Miq. subsp. **tristanensis** (Christoph.) Valdebenito *et al.*: 122 (1990).

Peperomia tristanensis Christoph.: 5 (1944).

Restricted to a small side gulley ± 200 m upstream from the top of the Waterfall. Six small plants were found, all growing in a wet, deeply shaded gulley, with no sign of flowers or fruit in March. Several saplings apparently resulted from vegetative sprouting of branches that had been knocked off.

Distribution: I. *Ryan 126* (BOL).

PLANTAGINACEAE

* **Plantago major** L.: 112 (1753).

Common on soil slips, particularly on the west-facing scarp, and on mesic open areas above the beach, including seepages on cliffs and on the fringes of bogs at Blenden Hall. A few plants occur on the plateau rim at up to 500 m altitude. Two forms occur, differing in the density of hairs on the leaves.

Distribution: G, I, T. *Dean 791, 793, 846* (BOL); *Roux 2060* (NBG); *Ryan 81* (BOL).

POLYGONACEAE

* **Rumex acetosella** L. subsp. **angiocarpus** (Murb.) Murb.: 41 (1899).

Rumex angiocarpus Murb.: 46 (1891).

Collected from Salt Beach in 1873, but has not been found there subsequently (Wace & Holdgate 1976; pers. obs.). Preece *et al.* (1986) recorded it from Pig Beach Hill in 1982-83, which was not visited during this survey. We recorded it only from the river junction below Denstone Hill on the plateau at ± 220 m, where it was found in short *Blechnum penna-marina* heath and along the edge of a *Sphagnum* bog.

Distribution: G, I, T. *Ryan 83* (BOL).

R. frutescens Thouars: 38 (1808).

Occurs up to ± 450 m in tussock grassland and wet heath, but absent from fern bush. It is common along the back of the boulder beaches, but also occurs in wet areas along watercourses in *Spartina* tussock and growing on the mat of *Scirpus sulcatus* at Skua Bog. Its seeds are eaten by the endemic buntings.

Distribution: G, I, T. *Dean 781* (BOL); *Roux 2061* (NBG).

* **R. obtusifolius** L. subsp. **obtusifolius**

The most widespread introduced plant at Inaccessible, it is common at all altitudes in disturbed and marshy places. It colonizes soil slips and other disturbances including albatross nests. Over much of the plateau it is restricted to watercourses, and seldom penetrates undisturbed natural vegetation. It is not listed from Nightingale (Groves 1981), but has been recorded there (Wace & Dickson 1965; Wace 1967; Wace & Holdgate 1976), and is common along the path between the huts and the Ponds. The seeds are eaten by the endemic buntings.

Distribution: G, I, N, T. *Dean 785, 851, 869* (BOL); *Roux 2208* (NBG).

RANUNCULACEAE

Ranunculus muricatus L.: 555 (1753).

As the material collected is sterile it could not be identified positively. Nicholas (pers. comm.) suggested that it may also be *Hydrocotyle ranunculoides* L.f. However, this is the first record of this plant for Inaccessible Island. Uncommon, restricted to the southwestern edge of the plateau. It is scarce in wet heath, in rank grass and sedges with *Hydrocotyle capitata*, between Boulder Hill and Swale's Fell. Also occurs sporadically in wet spots next to whitechinned petrel burrows southeast of Molly Bog.

Distribution: I. *Dean 841* (BOL); *Ryan 110* (BOL).

RHAMNACEAE

Phylica arborea Thouars: 45 (1808).

Common from sea level up to ± 450 m. In the more sheltered parts of the island it is dominant, growing up to 5 m tall. Flowering occurs from late October to March, but most flower in December-January (at sea level) and January-February (on the plateau), with little synchronism between trees. Fruits develop throughout the year, ripening and releasing the seeds just prior to or during flowering. Stunted plants on the high western plateau do not flower. The fruits are an important food for the endemic Wilkins' bunting (*Neospiza wilkinsi*). Flies visit the odorous flowers and may effect pollination.

Distribution: G, I, N, T. *Dean 786, 870* (BOL); *Roux 2089, 2197* (NBG).

ROSACEAE

Acaena sarmentosa (Thouars) Carm.: 502 (1818).

Ancistrum sarmentosum Thouars: 44 (1808).

Common above 200 m in all plant associations. Occurs down to sea level at Waterfall Beach and to 100 m above Blenden Hall in Nelson's Gulch. It is most abundant in wet heath. In fern bush it is typically associated with areas disturbed by breeding birds, and is thus virtually absent from the Serengeti. Flowers mid-October to November, with seed heads present chiefly in December-January, although flowering occurs later on exposed ridges. The seeds bear recurved hooks and are frequently entangled in the plumage of yellow-nosed albatrosses (*Diomedea chlororhynchos*) and other sea birds.

Distribution: G, I, N, T. *Dean 814, 867* (BOL); *Roux 2106, 2198* (NBG).

A. stangii Christoph.: 7 (1944).

Fairly common above 400 m in *Blechnum penna-marina* and wet heath, where it often grows in rock crevices and cliffs. The leaves, flower heads and seeds are smaller than those of *A. sarmentosa*, and the seeds lack recurved barbs. Apparently flowers slightly later than does *A. sarmentosa*.

Distribution: endemic, G, I, T. *Ryan 90* (BOL).

* **Malus domestica** Borkh.: 1272 (1803).

Two groves of planted trees flourish in hollows behind Blenden Hall, and there are some trees at Salt Beach (Wace & Dickson 1965). Single plants occur behind the hut at Blenden Hall (two), and on the plateau above the West Road (one) and in Ringeye Valley (one). The species apparently is not invasive. Budding and flowering occurs in November, and fruit are ripe in March-April. A small grove is established near The Ponds on Nightingale Island.

Distribution: I, N, T. *Dean 812, 862, 877* (BOL).

RUBIACEAE

Nertera assurgens Thouars: 42, t. 11 (1808).

Occurs primarily above 200 m, although reaches sea level along a stream at Salt Beach. It is the most abundant *Nertera* in wet heath, and appears to prefer damper situations than *N. depressa*; in fern bush it grows in well-shaded sites. Fruits present in October, but these are scarce and may be left over from the previous season. Most fruits ripen in January–March. It has medium-sized, pale green leaves (not glossy) with crenulate margins.

Distribution: endemic, I, T. *Ryan 86* (BOL).

N. depressa Banks & Sol. ex Gaertn.: 124 (1788).

Occurs at all altitudes and in all plant associations. Near sea level it is common on moss grown rocks, slips and occasionally on cliffs. In fern bush it frequently occurs as an epiphyte on the caudices of *Blechnum palmiforme*, occasionally growing over the crown. However, it is scarce in wet heath. Fruits are present throughout the summer. It is distinguished from the other *Nertera* species by its small (< 5 mm long), entire leaves.

Distribution: G, I, N, T. *Dean 774, 853, 876* (BOL); *Roux 2057* (NBG); *Ryan 85* (BOL).

N. holmboei Christoph.: 13 (1944).

The scarcest *Nertera* on Inaccessible, restricted to the plateau where it is patchily distributed in fern bush. Typically occurs in the shade under *Blechnum palmiforme* or *Phylica arborea*, but also occurs in the open on the flanks of Swale's Fell. Apparently fruits later than other *Nertera* species, with the first ripe fruits appearing in March. It is distinguished by its large (typically >10 mm long), entire, glossy dark green leaves.

Distribution: endemic, I, N. *Dean 816, 873* (BOL); *Roux 2115* (NBG); *Ryan 87, 121* (BOL).

SALICACEAE

* **Salix babylonica** L.: 1048 (1753).

Two or three stunted trees grow in tall *Spartina* tussock at Salt Beach, with no sign of reproductive organs in February.

Distribution: I, T. *Ryan 94* (BOL).

SCROPHULARIACEAE

* **Veronica serpyllifolia** L.: 12 (1753).

Not listed by Groves (1981) from Inaccessible, but recorded by Wace & Dickson (1965) and Preece *et al.* (1986). It is common on exposed areas such as soil slips above Blenden Hall, especially the slips adjacent to the West Road and on the slump below the plateau edge north of the West Road. Isolated patches also occur at Boulder Hill and Swale's Fell.

Distribution: I, T. *Dean 809, 824* (BOL); *Roux 2183* (NBG); *Ryan 73, 111* (BOL).

SOLANACEAE

†**Physalis peruviana** L.: 1670 (1753).

Collected once from Inaccessible in 1938 during the Norwegian Expedition (Groves 1981). There are no other records for the Tristan group.

* **Solanum nigrum** L.: 186 (1753).

Relatively uncommon introduced species, found mainly between Blenden Hall and Warren's Cliff. Two individual plants were also found at Salt Beach and Waterfall Beach. Occurs on slips and adjacent to the West Road up to ± 200 m, but one plant was found on the western plateau rim in a bird-disturbed area at 450 m. Flowers October to March.

Distribution: I, T. *Dean 803* (BOL); *Roux 2080* (NBG).

* **S. tuberosum** L.: 185 (1753).

Not listed by Groves (1981), but reported by Wace & Dickson (1965). Potatoes were restricted to the immediate vicinity of the huts at Waterfall Beach, and were flowering in February.

Distribution: I, (T). *Ryan 93* (BOL).

Bothalia 22,1: 111–117 (1992)

Salt glands in flowering culms of *Eriochloa* species (Poaceae)

M.O. ARRIAGA*

Keywords: culm anatomy, *Eriochloa*, ion excretion, *Poaceae*, salt glands

ABSTRACT

Salt glands were found in *Eriochloa* (Paniceae-Poaceae): *E. montevidensis, E. pseudoacrotricha* and *E. punctata*. They occur on the culms, rachises and secondary ramifications of the inflorescence. The glands are bicellular structures with endodermal tissue at the base. They consist of a basal cell and an apical cell, which is a collecting chamber with a large pore at the top. It is proposed to conserve the term salt gland to designate excretory structures associated with endodermal collecting tissue. The elements present in the glands (detected by the use of X-ray micro-analysis) are: Na, Mg, P, S, Cl, K with an increase of the elements from the endodermal tissue to the cap cell. Because of energy needed to transport and excrete salts, salt glands are situated at the base of the inflorescence, which is the zone of maximal development of Kranz structure. It is inferred that *Eriochloa* is a facultative halophytic genus, derived recently from a halophytic ancestor.

UITTREKSEL

Soutkliere is aangetref by *Eriochloa* (Paniceae-Poaceae): *E. montevidensis, E. pseudoacrotricha* en *E. punctata*. Hulle kom voor op die halms, ragisse en sekondêre vertakkings van die bloeiwyse. Die kliere is tweesellige strukture met endodermale weefsel aan die basis. Hulle bestaan uit 'n basale sel en 'n apikale sel. Laasgenoemde is 'n versamelholte en het 'n groot porie op die punt. Daar word voorgestel dat die term soutklier slegs vir uitskeidstrukture geassosieer met endodermale versamelweefsel, gebruik word. Die elemente aanwesig in die kliere (opgespoor met behulp van X-straalmikroanalise) is: Na, Mg, P, S, Cl en K, met 'n toename in die elemente vanaf die endodermale weefsel na die mus-sel. As gevolg van energie wat vir vervoer en uitskeiding van soute benodig word, is soutkliere geleë aan die basis van die bloeiwyse, wat die streek van maksimale ontwikkeling van Kranz-struktuur is. Daar word afgelei dat *Eriochloa* 'n fakultatiewe halofitiese genus is en onlangs uit 'n halofitiese voorouer ontstaan het.

INTRODUCTION

Studies of the Kranz structure development in flowering culms of some species of *Eriochloa* (Arriaga 1990) revealed conspicuous structures in the transection. They correspond to secretory tissue (sensu Fahn 1979) and are salt glands.

Salts are continuously transported into plant shoots via the transpiration stream (Waisel *et al.* 1986). In plants growing in halophytic or semi-halophytic habitats, salt accumulation may eventually reach a hazardous level, and survival of plants may depend on reduction of the salt content of the shoot (Waisel 1972). Excretion of ions by specialized salt glands is a well-known mechanism for regulating the mineral content of the plant (Waisel 1972; Liphschitz *et al.* 1974).

Salt glands have been known and described for various plant species since the middle of the past century (Volkens 1884; Marloth 1887; Ruhland 1915; Sutherland & Eastwood 1916; Fahn 1979, 1988, 1990; Levering & Thomson 1971, 1972; Waisel 1972; Liphschitz *et al.* 1974; Liphschitz & Waisel 1974, 1982; Hong-bin *et al.* 1982; Oross & Thomson 1982; Waisel *et al.* 1986; Drennan *et al.* 1987, amongst others).

Salt glands have been described in 12 families of phanerogams (Liphschitz & Waisel 1982), and the Poaceae are unique in the monocotyledons in possessing these structures. Sixteen genera of the Chloridoideae and 17 of the Panicoideae have been shown to possess salt glands on both leaf surfaces (Liphschitz & Waisel 1982). In this work it is shown that salts glands occur in some species of *Eriochloa* and these epidermal appendages are described and illustrated. They occur on the culms, rachises and secondary ramifications of the inflorescence. Such glands present a new morphological type different from the graminoid salt glands previously described.

MATERIALS AND METHODS

Transverse sections of flowering culms were made from immediately below the inflorescence, the rachis and secondary ramifications. Both herbarium and fresh material was used. The herbarium material was restored and reconstituted by slow imbibition in warm water from 24 to 48 hours or in etanol-glycerol 1:1 from 48 to 72 hours. Sections were obtained either freehand or the material was embedded in wax and sectioned on a rotary microtome (for ontogenic studies). The sections were stained with Alcian Blue and Safranin (Cutler 1978) or Cresyl Violet (Dizeo de Strittmatter 1980).

Fluorescence microscopy was used for sections of herbarium material. On the basis of the results of Dizeo de Strittmatter (1986) and using Acridin Orange and Methylene Blue as fluorochromes in simple fluorochrome techniques and Acridin Orange-calcofluor in a combined technique, we were able to deduce the nature of the wall of the salt gland cells. Specimens were examined with a Zeiss fluorescence photomicroscope incorporating a high-pressure mercury vapor lamp HBO 50W, a BP 450-490 Blue exciter filter, a chromatic divisor FT 510 and a suppressing filter LP520.

Histochemical reactions were used to determine the nature of ions excreted from the glands. The presence of

* Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Angel Gallardo 470, (1405) Buenos Aires, Argentina.
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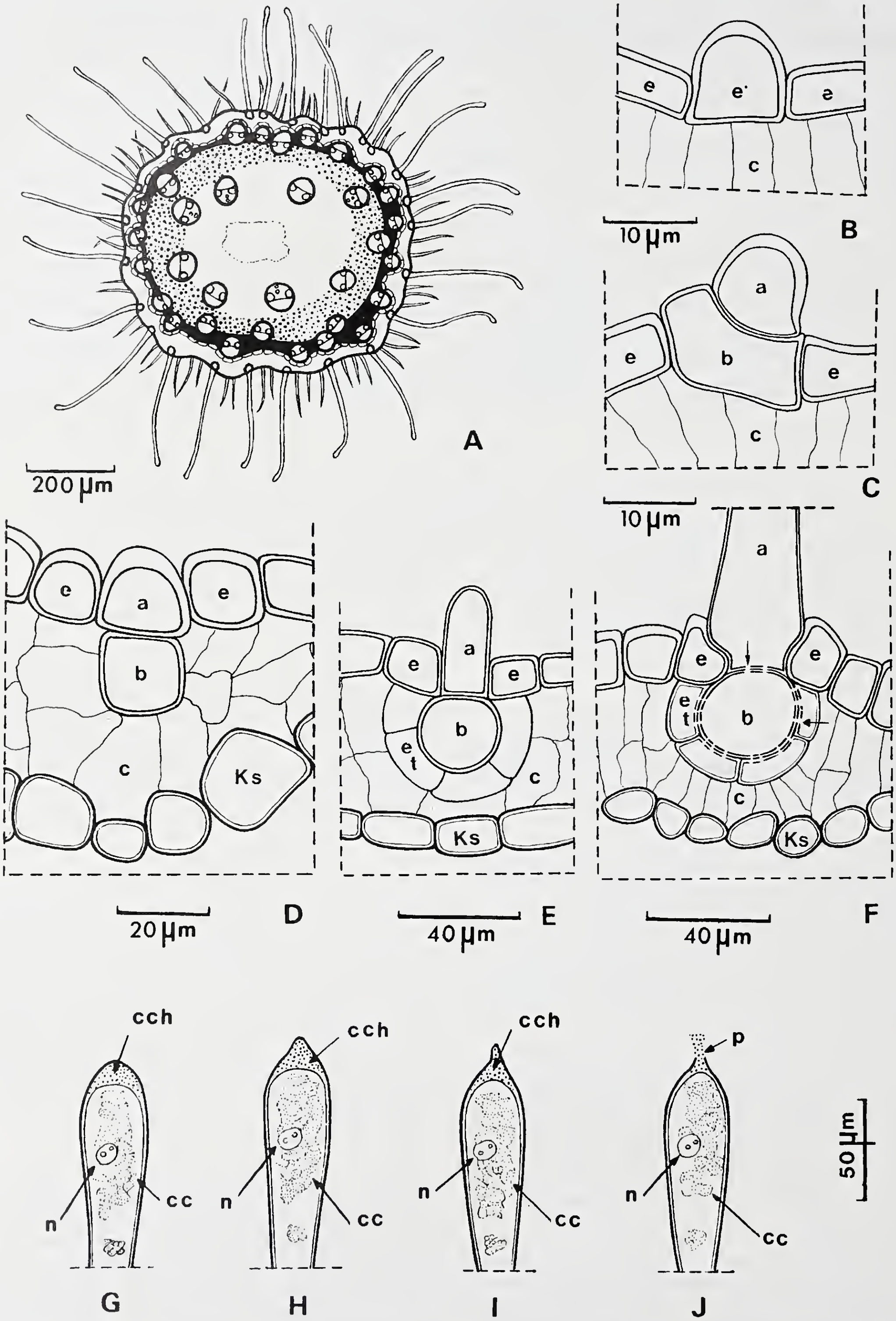

FIGURE 1.—A, *Eriochloa pseudoacrotricha, Saravia Toledo 1310,* t.s. of flowering culm of *Eriochloa* below inflorescence. B–F, *E. montevidensis, Pire s.n.*, ontogeny of salt gland: B, epidermal cell initiating differentiation; C, basal and apical cell formation; D, basal cell sunken beneath epidermal level, note also Kranz sheath; E, apical cell growing, shows differentiation of chlorenchyma surrounding basal cell to form endodermal tissue; F, mature salt gland, apical cell broken, endodermal tissue present with cutinization on cell walls and with pits connecting endodermal tissue with basal cell and this with apical cell. G–J, *E. punctata, Arriaga 584,* mature apical cell. a, apical cell; b, basal cell; c, chlorenchyma; cc, cytoplasm, denser in apex; cch, collecting chamber; e, epidermal cell; e', epidermal mother cell of salt gland; et, endodermal tissue; ks, Kranz sheath; n, nucleus; p, pore. Arrows show connection between cells.

Na was investigated using the technique described by Johansen (1940). The nature of the ions was also analysed and measured by X-ray micro-analysis in unfixed transections of culms, using a Phillips 515 SEM with an EDAX 9100 attachment. Photomicrographs were taken with Zeiss equipment and the schematic drawings were made with a Wild camera lucida.

Material examined

Eriochloa montevidensis

Baez 39 (BAB); *Saravia et al. 10072c* (CTES); *Venturi 702* (BA); fresh material: *Pire s.n.* cultivated Fac. Agronomía, UNRosario.

E. pseudoacrotricha

Lahitte & Castro 47614 (BAB); *Saravia Toledo 1310* (BA).

E. punctata

Ahumada 2570 (CTES); *Arriaga 312 & 576* (BA); *BA 61301*; *BAB 68290*; *Burkart 26145* (SI); *Cordini 106* (SI); *Pensiero 147* (SF); *Ragonese 3188* (SF); *Rodriguez 449* (BA); *Vegetti 442* (SF); fresh material: *Pire s.n.* cultivated Fac. Agronomía, UNRosario; *Arriaga 584* (BA).

RESULTS

Anatomical description of the salt glands

Culm transections of *Eriochloa* revealed a zone of excretory tissue near the base of the inflorescence. These epidermal appendages are much bigger than the macrohairs usually present in this genus (Figures 1A; 2A, B). These appendages consist of bicellular hairs associated with specialized cells at the base (Figures 1E, F; 2D, E).

These bicellular structures have a rounded basal cell, 35–45 μm in length, sunken into the chlorenchyma, and an elongated apical cell, 700–750 μm in length. The two cells meet at the level of the epidermal cells (Figure 1F). The walls of both cells are heavily cutinized (Figures 1F; 2D) and are distinct from the surrounding chlorenchyma tissue.

Numerous pit-like interruptions, and plasmodesmata are present in the cell walls between the basal cell and the apical cell and between the basal cell and the neighbouring chlorenchyma cells (Figures 1F; 2D). The specialized tissue present around the base of the salt gland is termed excretory endodermis, collecting tissue or endodermal tissue (Figure 1E, F). The endodermal tissue is not connected with the surrounding chlorenchyma by pits.

The distal part of the elongate apical cell is heavily cutinized and a subcuticular space forms between the wall and the cuticle during excretion (Figures 1G–J; 2F–H). This is a collecting chamber (Oross *et al.* 1985) where salt solutions accumulate. As the hydrostatic pressure within this compartment increases, it causes the pore aperture in the cuticle to open, allowing the fluid to flow to the surface.

In *Eriochloa* only one pore was observed at the top of the apical cell. During excretion a large drop is exuded. The increase in hydrostatic pressure in the collecting chamber initially causes the protrusion of the cuticula of the apex into a narrow structure resembling a finger, at the top of which the pore appears (Figures 1J; 2G, H). Obtuse and blunt but pointed (Lindley 1951) apices are therefore found in the distal cells of the salt glands in *Eriochloa* (Figure 2A–C).

Both basal and apical cells possess dense and granulose contents, and very conspicuous nuclei. The apical cell nucleus is displaced to the apical region where the cytoplasmatic contents are denser (Figures 1G–J; 2F–H). The basal and the apical cells, as well as those forming the endodermal tissue, are living cells with heavy cutinization of their walls. There is no direct connection between the salt glands and the vascular bundles.

The basal cell seems to function as a transport cell, whereas the excretion itself occurs at the apex of the apical cell (Figure 2H). These salt glands are present on the flowering culms, near the base of the inflorescence, on the rachis and the secondary ramifications. They were not observed on any other part of these plants.

These glands can be differentiated from the common macrohairs because they are more than 700 μm long and are associated with endodermal tissue at their base. Ordinary macrohairs are 125–250 μm long and are without endodermal tissue at their base, they are also unicellular structures.

Ontogeny of the salt glands

Salt glands are derived from an epidermal cell (Figure 1B), which divides periclinally to form two cells (Figure 1C). The inner cell sinks into the chlorenchyma during growth and differentiation (Figure 1D). It becomes rounded and its walls begin to be cutinized. The upper cell elongates and its walls are thickened by cutinization (Figure 1E). The walls of the neighbouring cells of the chlorenchyma surrounding the basal cell also become cutinized (Figure 1E, F).

The nuclei of the basal and apical cells become more and more conspicuous, the nucleus of the apical cell shifts towards the apex, and the cytoplasmic contents becomes denser and granulose (Figure 1G–J).

X-ray analysis of the contents of the salt glands

By running on a scanner line from the endodermal tissue up to the apical cell we determined by X-ray images the nature of ions present and their concentration gradients (Figure 3) in samples of flowering culms (*Pire s.n.*) of *Eriochloa punctata*. From the analysis of the graphics we conclude that: Na, K, Mg, P, S, Cl, are present, with K, and Cl the dominant elements.

The percentages of elements present are listed in Table I. Organic anions, nitrate and carbonate might be present as well but could not be detected by the microanalyser.

The presence of Ag is a result of the technique used in the coating of the samples for electron microscopy. An increase of Na, Mg and P from endodermal cell to apical cell was detected together with a decrease of S and K. Cl increases in the apical cell and decreases in endodermal tissue. The presence of Na in these salt glands was also confirmed by the use of the technique described in Johansen (1940).

The chemical nature of the thickening of the walls of the apical, basal and endodermal cells was investigated by the use of fluorescence microscopy. This thickening

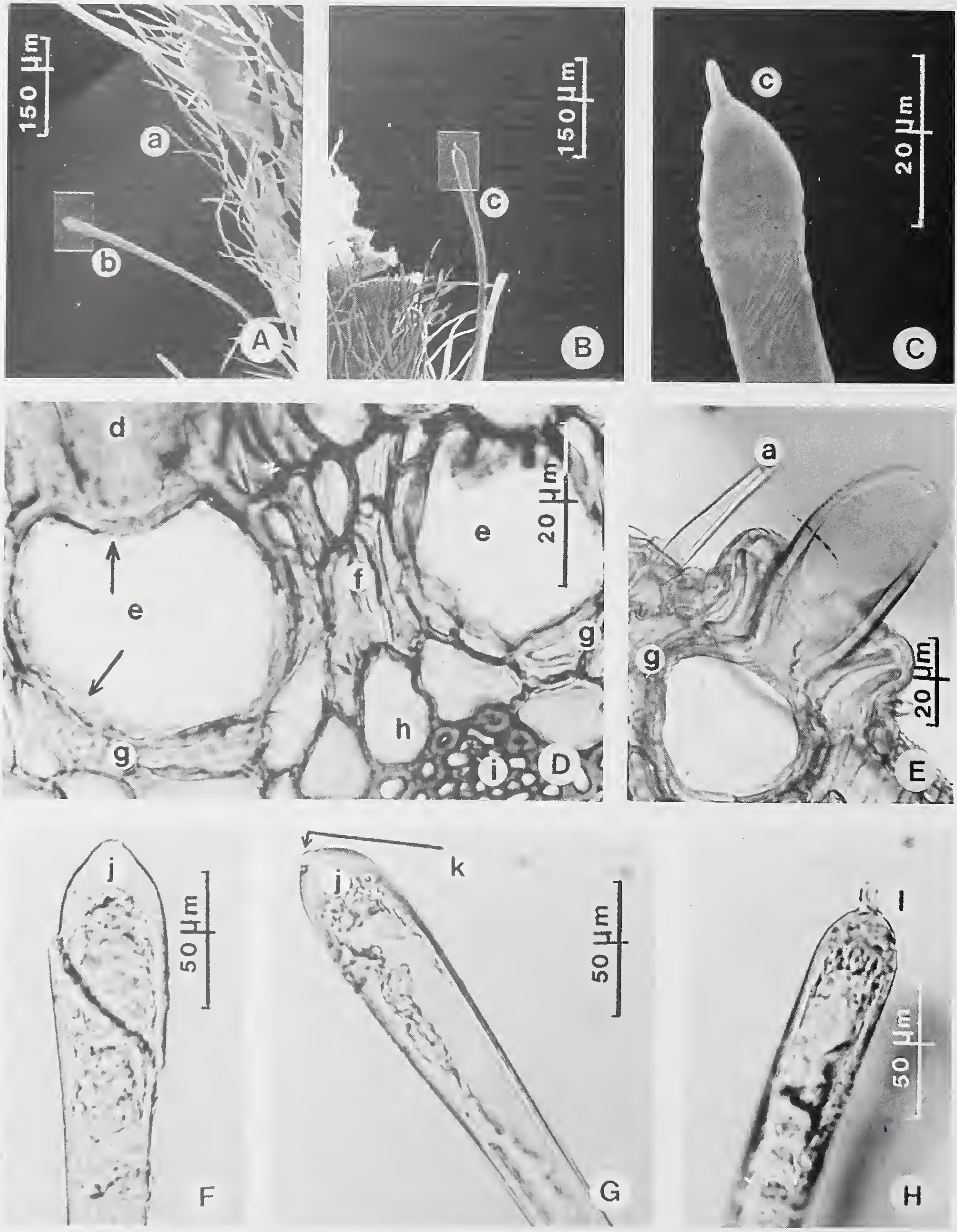

FIGURE 2.—A–C: *Eriochloa punctata, Pire s.n.*: A,B, SEM view of flowering culm below the inflorescence; C, SEM view of obtuse apex with acumen from a salt gland. D–H, LM views: D, basal cell surrounded by endodermal tissue and chlorenchyma; E, salt gland in an intermediate state of development with apical cell growing and endodermal tissue forming; F, G, H, distal zone of apical cell. a, macrohair; b, salt gland with obtuse apex; c, salt gland with a pointed apex; d, apical cell; e, basal cell; f, chlorenchyma; g, endodermal tissue; h, Kranz sheath; i, vascular bundle; j, collecting chamber; k, pore; l, pore excreting. Arrows show connection between cells. D, *E. punctata, BA 61301*; E, *E. montevidensis, Venturi 702*; F–H, *E. punctata, Arriaga 584.*

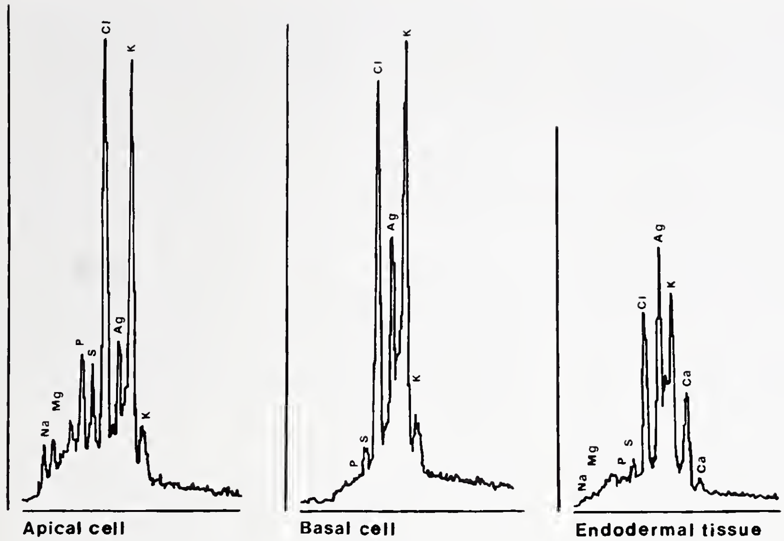

FIGURE 3.—Energy dispersive X-ray diagrams of the analysis of a salt gland.

results from the presence of cutin in the wall, with more cutinization in the base and distal zone of the apical cell.

DISCUSSION

The structure of salt glands varies greatly in different plant species but is usually similar in plants of the same genus or even within a family (Waisel 1972; Liphschitz *et al.* 1974). Based on their structural organization, there are three types of salt glands (Thomson 1975; Fahn 1979, 1988, 1990): the two-celled glands of the grasses, the bladder cells of the Chenopodiaceae and the multicellular glands which occur in other dicotyledonous families. The salt glands described for some species of *Eriochloa* do not coincide with the morphological type described for the Poaceae. Despite being bicellular structures they resemble a macrohair and not a typical microhair. They possess endodermal tissue at the base which is thought to prevent the flow of the excreted substances back into the plant. When the endodermal tissue is differentiated, it is structurally closer to that of the salt glands described for dicotyledons.

Retaining the original terminology of Waisel (1972) and Fahn (1979), it is proposed to restrict the term salt gland to the excretory structures associated with collecting tissues (i.e. endodermal tissue) and to reserve the term salt hairs (or salt pumps) for the excreting microhairs known in grasses.

Three fundamental features determine the effectiveness of salt glands in removing excess salt: a, their structure, location and abundance; b, their mechanism; c, their physiological and ecological significance (Waisel 1972). The basal cell of the salt hairs of grasses is sunken into the epidermis, located above it, or in intermediate positions. By contrast, the basal cell of the salt glands of *Eriochloa* is completely sunken into the chlorenchyma. As seen from data presented in Liphschitz & Waisel (1982) the more sunken the gland, the higher its excretion efficiency. Furthermore, a close relationship can also be found between excretion efficiency and basal cell dimensions. This suggests that the salt glands of *Eriochloa* are very efficient in excreting as they have a big, round basal cell completely sunken into the culm.

Spartina foliosa (Levering & Thomson 1971) and *Spartina anglica* (Hong-bin *et al.* 1982) have no cuticular layer separating the mesophyll from the salt hair. In *Eriochloa* the walls of the endodermal tissue are cutinized, as are the walls of the basal and apical cells.

At the apex of salt glands, between the cellulose layer of the wall and the cuticle, a subcuticular space is formed during excretion (collecting chamber). When pressure reaches a certain value, pores in the cuticle open, and droplets appear on the surface (Oross *et al.* 1985; Fahn 1990). In *Eriochloa* salt glands, a collecting chamber is visible at the top of the apical cell, but only one large pore is developed.

Within the Poaceae, in the Chloridoideae, ultrastructural studies of these two-celled structures have only been reported for three genera: *Spartina* (Levering & Thomson 1971, 1972), *Cynodon* (Oross & Thomson 1982) and *Distichlis* (Oross & Thomson 1982; Oross *et al.* 1985).

Although genera of the Panicoideae with excretory activity have been reported, these microhairs lack partitioning membranes in their basal cells (Amarasinghe & Watson 1988). Ultrastructural studies are required to determine whether *Eriochloa* species have these plasmalemma invaginations.

TABLE 1.—Percentages of elements present in salt glands

Element	Endodermal cell	Basal cell	Apical cell
Na	2.99%	none detected*	6.85%
Mg	1.29%	none detected*	3.95%
P	2.21%	0.84%	6.75%
S	5.02%	3.33%	4.48%
Cl	31.33%	38.30%	33.24%
K	57.16%	57.52%	44.77%

* too low to be measured.

Despite the fact that salt glands are best known on epidermal surfaces of leaf blades, they can sometimes be observed on epidermal surfaces of lemmas, paleas and lodicules. This is the first report of salt glands on the culms, as well as the rachis and secondary ramifications of Poaceae.

From this study it is not possible to indicate how excreted substances flow to the exterior. But it can be inferred in the light of Fahn's (1988) statement that these substances are excreted symplastically. Fahn (1988) pointed out the presence of complete cutinization of the walls on cells of the salt glands and endodermal tissue which 'indicates that the flow of excretory substances or their precursors takes place exclusively through the symplast and that flow of the excreted substances back into the plant through the apoplast is prevented'.

Ions reported as occurring in the excreted solutions of salt glands are: Na^+, K^+, Mg^{++}, Ca^{++}, Cl^-, $SO_4^=$, NO_3^-, $PO_4^=$ and HCO_3^- (Waisel *et al.* 1986; Fahn 1988). It was possible to analyse and measure ions present in the cap cell, the basal cell and in cells from the endodermal tissues in *Eriochloa punctata* by the use of an X-ray micro-analyser. The elements present were: Na, Mg, P, S, Cl, K, with a general increase of the elements from the endodermal tissue to the cap cell.

It is known that salinity induces changes in leaf anatomy increasing its leaf thickness and generally reducing photosynthesis and lowering the resistance to CO_2 intake (Longstreth & Nobel 1979), but no leaf succulence was observed in the *Eriochloa* species studied.

A possible relationship between photosynthesis and excretion is suggested by the work of Hill & Hill (1973). They proposed that ATP derived from respiration and possible cyclic photophosphorylation in the light is utilized in the excretion process. Since the glands do not have chloroplasts, the authors suggested that in the light the ATP would be derived from the mesophyll and diffuse symplastically to the glands. Moreover salts are transported outward, against a concentration gradient, by specific mechanisms which consume metabolic energy (Waisel 1972).

The siting of salt glands in *Eriochloa*, on culms at the base of the inflorescence, in rachis and secondary ramifications, coincides with the zone of maximal development of Kranz structure (Arriaga 1990), (zone of maximal efficiency in photosynthesis also), and would correspond to a need for high amounts of energy to transport and excrete salts by salt glands.

Salt glands in *Eriochloa* are derived directly from epidermal tissue and occur with other externally similar emergences such as 'normal' macrohairs. Patterson (1982) argues that homologous structures cannot occur in the same organism, so the glands cannot be homologous with the macrohairs. The same criterion was used by Linder *et al.* 1990 in connection with *Pentachistis* glands and other epidermal emergences.

The salt glands described here are excretory organs typical of many non-succulent halophytic species (Liphschitz & Waisel 1974). Some glands appear in species that today occupy rather non-saline environments. Excretion occurs in such plants only when they are transferred from the glycophytic to the semihalophytic or halophytic habitat (Liphschitz & Waisel 1982). In other plant species addition of salt to the growth medium affected the number of glands (Rosema *et al.* 1977). Although *Eriochloa* is not considered to be a halophytic genus, plants of this genus sometimes live in saline environments or saline patches, sometimes cohabiting with halophytic genera (i.e. *Distichlis*).

Eriochloa is a C_4 genus (Brown 1977; Ellis 1977; Hattersley 1982; Watson *et al.* 1986; Sánchez & Arriaga 1990). Many C_4 plants have been shown to tolerate Na and they frequently seem to be either halophytes or of halophytic origin (Liphschitz & Waisel 1974). The primary adaptation of C_4 plants was probably to saline environments (Laetsch 1974).

The existence of salt glands in a species which at present occupies non-saline habitats indicates that it probably originated as a halophyte and that, sometime in the past, its ancestors occupied saline habitats (Liphschitz *et al.* 1974). Though some species remained in saline habitats, most species migrated later from saline to non-saline habitats. Such migration probably occurred not too long ago, as those plants still retain many characteristics of their halophytic ancestors (Liphschitz & Waisel 1982). The existence of semisunken glands in plants which presently occupy non-saline habitats also suggests that the change from a halophytic to a glycophytic character, occurred only recently (Liphschitz & Waisel 1974). From all the points discussed above we infer that *Eriochloa* derives from a halophytic ancestor and is of recent origin.

Liphschitz & Waisel (1982) are of the opinion that species belonging to the Panicoideae and Chloridoideae have evolved from closely related ancestors which occupied saline (coastal?) habitats. The occurrence of salt glands (salt hairs) in 18 genera of Chloridoideae (Liphschitz & Waisel 1982; Taleisnik & Anton 1988; Marcum & Murdock 1990), with only three of them belonging to genera presently occupying saline habitats, and in 18 genera of Panicoideae, all of them at present occupying non-saline habitats, would lend support to this hypothesis.

It is obvious that salt glands in *Eriochloa* allow it to behave as a facultative halophytic genus, establishing it as an important candidate for economic utilization of saline environments.

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Invasive alien woody plants of the eastern Cape

L. HENDERSON*

Keywords: alien invasive plants, eastern Cape, Fynbos Biome, Grassland Biome, Nama-Karoo Biome, roadside survey, Savanna Biome

ABSTRACT

The frequency and abundance of invasive alien woody plants were recorded along roadsides and at watercourse crossings in 69.9% (151/216) of the quarter degree squares in the study area. The survey yielded 101 species of which the most prominent (in order of prominence) in roadside and veld habitats were: *Opuntia ficus-indica, Acacia mearnsii* and *A. cyclops*. The most prominent species (in order of prominence) in streambank habitats were: *A. mearnsii, Populus* × *canescens, Salix babylonica* and *S. fragilis* (fide R.D. Meikle).

The greatest intensity of invasion was recorded in the wetter eastern parts and particularly in the vicinity of Port Elizabeth, Uitenhage, East London, Grahamstown, Hogsback and Stutterheim. There was relatively little invasion in the central and western dry interior except along watercourses.

UITTREKSEL

Die frekwensie en voorkomsdigtheid van uitheemse houtagtige indringerplante is langs paaie en by oorgange oor waterlope in 69.9% (151/216) van die kwartgraadvierkante in die studiegebied aangeteken. Daar is 101 spesies aangetref waarvan die mees prominente (in volgorde van prominensie) langs paaie en in veldhabitats, *Opuntia ficus-indica, Acacia mearnsii* en *A. cyclops* was. Die mees prominente spesies (in volgorde van prominensie) langs stroomoewers, was *A. mearnsii, Populus* × *canescens, Salix babylonica* en *S. fragilis* (fide R.D. Meikle).

Die ergste indringing is in die vogtiger oostelike gebiede aangetref, veral in die omgewing van Port Elizabeth, Uitenhage, Oos-Londen, Grahamstad, Hogsback en Stutterheim. Behalwe langs waterstrome, was daar betreklik min indringing in die sentrale en westelike droë binneland.

CONTENTS

INTRODUCTION

Survey history and objectives

This study of the eastern Cape is the fifth of eight regional surveys which together are designed to reflect invasion by woody alien plants in the Republic of South Africa as a whole. Surveys have been completed for the Transvaal (Henderson & Musil 1984), Natal (Henderson 1989), Orange Free State (Henderson 1991a) and northern Cape (Henderson 1991b). This survey of the eastern Cape was undertaken in March, October and November 1988 and March 1990.

The objectives of the survey are: to produce a checklist of the major invasive alien woody plants of streambank, roadside and veld habitats in the study area; to determine the pattern of alien woody invasion as a whole and for individual species; to attempt to relate distribution to environmental factors and to determine which are the most prominent and potentially important invaders.

The study area

The study area lies between latitudes 30° and 34°S and 23° and 29°E (Figure 1). The altitude rises in successive terraces from sea level on the Indian Ocean in the south and southeast to 3 000 m in the Drakensberg in the northeast. Four major physical divisions can be delimited (Nicol 1988). These are the coastal subregion stretching inland

* Plant Protection Research Institute, Dept of Agricultural Development; stationed at National Botanical Institute, Private Bag X101, Pretoria 0001.
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FIGURE 1.—The study area, showing the major physical features, and its relation to surrounding territories.

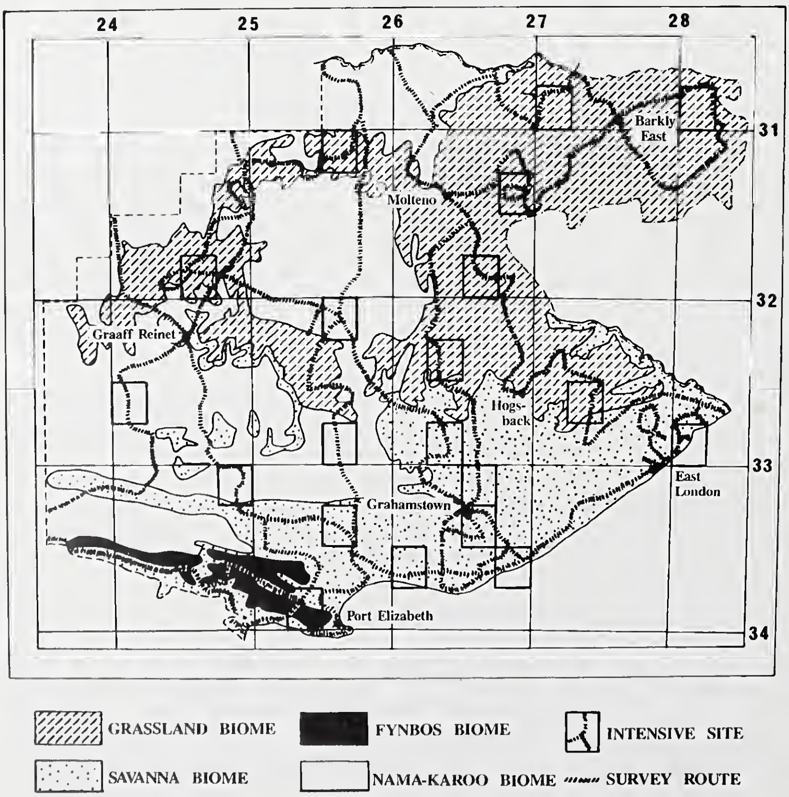


FIGURE 2.—The study area, showing its biomes (Rutherford & Westfall 1986), survey routes and intensive sites.

to the 300 m contour; the southern coastal mountains up to 1 500 m high lying west, north and northeast of Port Elizabeth; the midland region which is hilly to mountainous country and includes the Winterberg with a maximum height of 2 369 m; and the northern mountain region which extends from the Sneeuberg in the west to the Stormberg and Drakensberg in the east. Seven major river systems arise in, and drain, the study area.

Rainfall ranges from 150 mm per annum in the extreme western interior to 1 700 mm in the Amatole Mountains (Dent *et al.* 1989). Most of the western and central regions receive less than 500 mm per annum (Kopke 1988). The seasonal distribution of rainfall ranges from a winter maximum on the coast between Port Elizabeth and Port Alfred through to a summer maximum in the northern interior (Kopke 1988).

Temperatures vary greatly from the coast inland. The coastal zone is mild in both winter and summer (Kopke 1988). The climate becomes progressively more temperate towards the arid west and with increasing altitude in the north. The interior above the Winterberg escarpment is characterized by hot summers, cold winters and widespread frost (Kopke 1988). Snow has been recorded occasionally for a few localities at low altitudes (e.g. Grahamstown) and is regular in mountainous parts (Gibbs Russell & Robinson 1981).

Four major vegetation units or biomes and 21 vegetation categories have been described in the eastern Cape by Lubke *et al.* (1986). For the purposes of this survey and in keeping with previous surveys, the vegetation of the study area has been subdivided according to the biomes of southern Africa defined by Rutherford & Westfall (1986) and Acocks's *Veld types of South Africa* (1988). The Grassland, Savanna, Fynbos and Nama-Karoo Biomes converge in the eastern Cape (Figure 2). Twenty-six Acocks Veld Types occur in the study area and have been grouped into seven broad veld type categories for the purposes of this survey (Table 1 and Figure 3).

Temperate grassland occupies the highest and coldest parts of the study area at elevations of 1 500 m to 3 000 m. Rainfall ranges from 300 mm in the west to 1 000 mm in the extreme northeast. Moist subtropical grassland occurs on the cool and wet eastern and southeastern slopes of the Drakensberg at elevations from 600 m to 2 000 m. Rainfall ranges from 500 mm to 1 700 mm. Pockets of Afromontane forest occur in favourable localities.

Coastal 'forest' occupies the mild coastal belt with an annual rainfall ranging from 600 mm in the south to 1 000 mm in the north. Vegetation types occurring in this zone are forest, dune thicket, Acacia savanna, grassland and littoral strand vegetation (Lubke *et al.* 1986). Subtropical thicket and savanna occurs from sea level to about 1 500 m. Rainfall ranges from 200 mm in the hot and dry river valleys to 900 mm on the foothills of the Winterberg.

Fynbos shrublands, hereafter referred to broadly as mountain fynbos, occur along the tops and slopes of the southern coastal mountains at an altitude ranging from 300 m to 1 500 m. Small outliers are situated within the Savanna Biome along the Suurberg and on the Grahamstown hills. Rainfall ranges from 500 mm to 900 mm per annum.

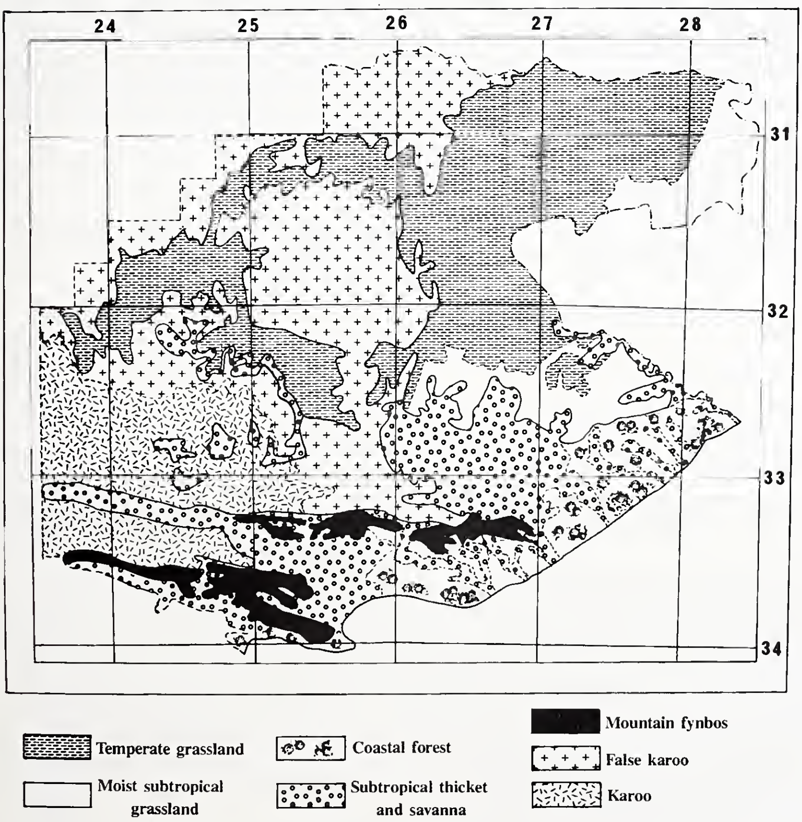


FIGURE 3.—The seven broad veld type categories in the study area (after Acocks 1988).

TABLE 1.—Veld type categories in the study area and the equivalent Acocks Veld Type groupings and Veld Type numbers

Biome† and veld type category*	Acocks Veld Type grouping	Acocks Veld Type No.
Grassland Biome		
Temperate grassland	VI. Pure Grassveld Types	48, 50, 58, 59, 60
	IIIA. False Bushveld Types	22
Moist subtropical grassland	V. Temperate and Transitional Forest and Scrub Types	44
Savanna Biome		
Coastal 'forest'	I. Coastal Tropical Forest Types	1, 2, 7
Subtropical thicket and savanna	IV. Karoo and Karroid Types	23, 24, 25, 26
	IIIA. False Bushveld Types	21
	IVA. False Karoo Types	36, 37
Fynbos Biome		
Mountain fynbos	VIIA. False Sclerophyllous Bush Types	70
Nama-Karoo Biome		
False karoo	IVA. False Karoo Types	36, 37, 38, 42
Karoo	IV. Karoo and Karroid Types	24, 25, 26, 30, 31

* according to Henderson; † according to Rutherford & Westfall 1986.

False karoo, at an altitude of between 1 000 m and 1 500 m, occupies areas formerly covered by grassland. Annual rainfall ranges from 200 mm to 500 mm. Karoo or dwarf shrubland occupies the very arid and western interior at an altitude of between 500 m and 1 000 m with an annual rainfall of between 150 mm and 400 mm.

METHOD

Sampling method

The method used in this survey was basically the same as that used in previous surveys. The changes to the abundance scale for streambank habitats adopted by Henderson (1991b) have also been followed here (see next subheading). The presence and abundance of all alien trees, large shrubs and conspicuous climbers which appeared to be spreading spontaneously (naturalized) were recorded for each veld type category, habitat type (roadsides and adjoining veld, and streambanks) and quarter degree/fifteen minute square traversed by road. Twenty quarter degree squares were selected for more intensive surveying (Figure 2). They may be used at a later date for a quick resurvey of the study area to assess any changes that may have taken place.

Recordings of roadside and veld invaders were made from a moving vehicle along road transects of between five and ten kilometres in length. The average transect length was 7.3 km for the general survey area and 5.0 km for intensive sites. Recordings of streambank invaders were made at virtually all watercourse crossings on the road transects. Details of the roads traversed are lodged in the P.P.R.I., Pretoria. As on previous occasions the survey was undertaken in a minibus, with one driver and one recorder (the author). The average speed was 60 km/h but ranged from about 20 km/h in densely vegetated areas to 100 km/h in sparsely vegetated areas.

Abundance ratings

The abundance ratings for roadside and veld habitats and streambank habitats are given in Table 2.

TABLE 2.—Abundance ratings

Rating	Roadsides and veld	No. *	Streambanks	Rating
9	A virtually continuous, almost pure stand	1000+	Any number, with cover more than 75% of the reference area	7
8	The commonest species in a generally continuous tree or shrub layer	500–999	Any number, with 50–75% cover	6
7	Less abundant than above but greater than 20 individuals or groups per km	200–499	Any number, with 25–50% cover	5
			Any number, with 5–25% cover	4
6	10–20 individuals or groups per km	100–199	Numerous, but less than 5% cover or scattered, with cover up to 5%	3
5	5–10 individuals or groups per km	50–99		
4	2–5 individuals or groups per km	20–49	Few, with small cover	2
3	± 1 individual or group per km	5–19	Solitary, with small cover	1
2	Less abundant than above but more than 1 individual or group per 5 km	2–4		
1	± 1 plant or group per 5–10 km	1		

* approximate numbers of individuals or groups per 10 km transect.

Sampling level achieved

The sampling level achieved was 69.9% (151 out of the total 216 quarter degree squares) at an average of 29.9 km travelled per square. An average of 18.5 km of road transects were sampled per quarter degree square for abundance estimates of roadside and veld invaders. The mean surface area of each of the quarter degree squares, in which 20 intensive sampling sites are situated, is 646 km² (23.39 × 27.62 km).

The veld type coverage in terms of quarter degree squares and road transects sampled, kilometres travelled and watercourse recordings made, is given in Table 3. Statistics for streambank, roadside and veld habitats are given in Tables 4 & 5.

Data treatment—formulae used

Frequency

The percentage frequency of occurrence of a species x in a given category (veld type, biome or study area) y was calculated as follows:

$$\text{frequency} = \frac{\text{no. of watercourse recordings/road transects in category y having species x}}{\text{total no. of watercourse recordings/road transects in category y}} \times 100$$

Prominence value

The prominence value is a combined measure of a species' frequency and abundance relative to that of all other species, within a given vegetation category (veld type, biome or study area).

In streambank habitats the prominence value for a species x in category y was calculated as follows:

$$\text{prominence value} = \frac{\text{total weighted abundance of species x in category y}}{\text{sum of the weighted abundances of all species in category y}} \times 100 + \frac{\text{frequency of species x in category y}}{\text{sum frequency of all species in category y}} \times 100$$

The abundance ratings were weighted according to the minimum percentage cover in each scale rating (see Table 2). Thus ratings 7, 6, 5 and 4 had weighted values of 75, 50, 25 and 5 respectively. Ratings 1, 2 and 3 each had weighted values of 1.

In roadside and veld habitats the prominence value for a species x in category y was calculated as follows:

$$\text{prominence value} = \frac{\text{total abundance* of species x in category y}}{\text{sum of the abundances* of all species in category y}} \times 100 + \frac{\text{frequency of species x in category y}}{\text{sum frequencies of all species in category y}} \times 100$$

The highest prominence values in a given category which add up to approximately 160 points out of a total of 200 are printed in bold in Tables 6, 7, 8 and 9. The cut-off point of 160 points is arbitrary but represents 80% of the summed prominence values.

Mean species abundance rating in roadside and veld habitats (see Tables 8 and 9)

The mean species abundance rating** of a species x in a given category (veld type, biome or study area) y was calculated as follows:

$$\text{mean no. of individuals or groups per 10 km} = \frac{\text{total no. of individuals or groups of species x in category y}}{\text{total distance along which species x was rated in category y}} \times 10$$

Mean abundance of invaders per km in roadside and veld habitats (see Table 5)

The mean abundance of invaders per kilometre in a given category (veld type, biome or study area) y/quarter degree square z was calculated as follows:

$$\text{mean abundance} = \frac{\text{total abundance* of all species in category y/quarter degree square z}}{\text{total kilometres rated for abundance estimates in category y/quarter degree square z}}$$

RESULTS

The survey yielded 101 naturalized alien species. These species are listed in the Appendix together with a further 29 species which were obtained from various literature and other sources. The distributions of 30 of the most prominent species are given in Figures 7 and 8.

The streambank habitat

The whole study area

Six hundred and thirty-eight watercourse crossings were sampled in which 72 species were recorded, with up to nine species in one sample. Invaders were present at 61.0% of all crossings and 9.1% of all crossings were heavily invaded (Table 4).

Analysis according to veld type

Invasion was intense in both mountain fynbos and moist subtropical grassland where the highest percentages of river crossings were recorded as invaded and heavily invaded. The greatest number of species was recorded in subtropical thicket and savanna but few crossings were heavily invaded in this veld type category. Overall the Fynbos Biome was the most heavily invaded in terms of percentage crossings invaded and percentage crossings

* each abundance rating was expressed in numbers of individuals or groups recorded per transect (see Table 2). To be both conservative and consistent the minimum number was used in each instance, e.g. an abundance rating of 5 over ten kilometres = 50 and an abundance rating of 5 over five kilometres = 25.

** mean no. of individuals or groups per 10 km converted to rating (see Table 2).

TABLE 3.—Sampling coverage of each biome, veld type category and the study area

Biome‡ and veld type category†	1/4 degree squares	Road transects	Distance (km)*	Watercourse recordings
Grassland Biome	64	128	978	215
Temperate grassland†	52	98	785	188
Moist subtropical grassland†	19	30	193	27
Savanna Biome	65	147	998	231
Coastal 'forest'†	30	62	343	56
Subtropical thicket and savanna†	51	85	655	175
Fynbos Biome	10	15	90	16
Mountain fynbos†	10	15	90	16
Nama-Karoo Biome	57	94	725	176
False karoo†	46	66	532	131
Karoo†	12	28	193	45
Study area	151	384	2791	638

* this represents the distance along which abundance recordings were made. Total distance along which observations were made is approximately one and a half times that given; † according to Henderson; ‡ according to Rutherford & Westfall 1986.

TABLE 4.—Statistics for streambanks in each veld type category, biome and the study area

Biome‡ and veld type category†	Total no. of spp.	Average no. of spp./crossing	Max. no. of spp./crossing	% crossings heavily invaded*	% crossings invaded**
Grassland Biome	39	1.5	6	17.7	74.0
Temperate grassland†	31	1.4	6	13.8	70.7
Moist subtropical grassland†	21	2.3	6	44.4	96.3
Savanna Biome	45	1.5	9	3.0	59.3
Coastal 'forest'†	27	2.2	8	3.6	80.4
Subtropical thicket and savanna†	38	1.3	9	2.9	52.6
Fynbos Biome	19	2.0	5	68.8	93.8
Mountain fynbos†	19	2.0	5	68.8	93.8
Nama-Karoo Biome	24	0.7	9	1.1	44.3
False karoo†	20	0.8	9	1.5	47.3
Karoo†	10	0.5	4	0.0	35.6
Study area	72	1.3	9	9.1	61.0

* one or more species scored an abundance rating of 5 or more; ** invaders present; † according to Henderson; ‡ according to Rutherford & Westfall 1986.

TABLE 5.—Statistics for roadside and veld habitats in each veld type category, biome and the study area

Biome‡ and veld type category†	Total no. of spp.	Average no. of spp./ 1/4° sq.	Max. no. of spp./ 1/4° sq.	% transects invaded	% transects heavily invaded*	Mean abundance of invaders per km**
Grassland Biome	54	6.0	18	100.0	21.1	3.4
Temperate grassland†	40	5.1	13	100.0	15.3	2.2
Moist subtropical grassland†	37	7.1	18	100.0	40.0	8.0
Savanna Biome	62	7.2	20	98.0	44.9	8.3
Coastal 'forest'†	48	8.5	19	96.8	45.2	9.9
Subtropical thicket and savanna†	43	5.6	12	98.8	44.7	7.4
Fynbos Biome	31	8.8	19	93.3	73.3	23.8
Mountain fynbos†	31	8.8	19	93.3	73.3	23.8
Nama-Karoo Biome	29	4.4	13	96.8	4.3	1.4
False karoo†	29	4.5	13	95.5	4.5	1.4
Karoo†	9	4.2	8	100.0	3.6	1.3
Study area	94	7.3	25	98.2	28.1	5.3

* one or more species scored an abundance rating of 5 or more; ** see data treatment—formulae used; † according to Henderson; ‡ according to Rutherford & Westfall 1986.

heavily invaded. The Grassland Biome was the next most heavily invaded followed by the Savanna Biome and lastly the Nama-Karoo Biome (Table 4).

Analysis according to species

Frequency

Salix babylonica was the most frequently recorded invader in the study area (19.6%). Only this species and *Populus* × *canescens* (11.8%) were recorded at 10% or more crossings in the whole study area (Table 7).

In the Fynbos Biome the most frequently recorded species were *Acacia mearnsii* (75.0%), *A. saligna* (37.5%) and *Populus* × *canescens* (31.3%). In the Nama-Karoo Biome *Salix babylonica* (13.1%) was the most frequent invader. In the Grassland Biome the most frequently recorded species were *S. babylonica* (44.2%), *Populus* × *canescens* (27.9%) and *S. fragilis* (20.9%). In the Savanna Biome the most frequently recorded species was *Ricinus communis* (22.5%).

Other species which were recorded at 10% or more crossings in a veld type category were: *Acacia cyclops* and *Eucalyptus* spp. in mountain fynbos; *Atriplex* cf. *nummularia* in karoo; *Acacia dealbata, A. mearnsii, Prunus persica* and *Salix caprea* in moist subtropical grassland; *A. cyclops, A. mearnsii, Cestrum laevigatum, Sesbania punicea* and *Solanum hispidum* in coastal 'forest'; and *Arundo donax* and *Nicotiana glauca* in subtropical thicket and savanna.

Prominence

The most prominent invader in the whole study area was *Acacia mearnsii* with a prominence value of 32.2 out of a combined total for all species of 200 (Table 7). The next most prominent invaders were *Populus* × *canescens* (28.7) and *Salix babylonica* (28.2).

In the Fynbos Biome *Acacia mearnsii* was by far the most prominent invader followed by *Populus* × *canescens* and *A. saligna*. In the Nama-Karoo Biome *Atriplex* cf. *nummularia* was the most prominent invader in the karoo veld type category. *Salix babylonica* was the most prominent invader in false karoo and the whole of the Nama-Karoo Biome.

In the Grassland Biome *Salix babylonica, Populus* × *canescens* and *S. fragilis* were the most prominent invaders. The same species were also the most prominent invaders in temperate grassland. *Acacia mearnsii, S. babylonica* and *A. dealbata* were the most prominent invaders in moist subtropical grassland.

In the Savanna Biome *Sesbania punicea, Arundo donax, Ricinus communis* and *Acacia mearnsii* were the most prominent invaders. *A. cyclops* was most prominent in coastal 'forest' and *Arundo donax* was most prominent in subtropical thicket and savanna.

Roadside and veld habitats

The whole study area

One hundred and fifty one quarter degree squares and 384 road transects were sampled in which 94 species were recorded. Up to 25 species were recorded per quarter degree square. Naturalized species were recorded in 98.2% of all transects sampled and 28.1% of all transects were heavily invaded (Table 5).

Analysis according to veld type

Invasion was most intense in mountain fynbos where the highest percentage of transects was heavily invaded and the mean abundance of invaders per km reached a maximum (Table 5). The next most heavily invaded categories were coastal 'forest', subtropical thicket and savanna, and moist subtropical grassland. The greatest number of species was recorded in coastal 'forest'.

Analysis according to species

Frequency

The most frequently recorded species in the whole study area were *Opuntia ficus-indica* (67.4%), *Agave americana* (28.4%), *O.* cf. *robusta* cultivars (26.8%) and *Acacia mearnsii* (20.3%) (Table 9). Other species which were recorded in 10% or more transects were *Acacia cyclops, Eucalyptus* spp., *Nicotiana glauca, Prunus persica, Ricinus communis* and *Rosa eglanteria*.

The most frequently recorded species in the Fynbos Biome were *Acacia mearnsii, A. cyclops, Eucalyptus* spp. and *Opuntia ficus-indica*. In the Nama-Karoo Biome, *O. ficus-indica, O.* cf. *robusta* cultivars and *Agave americana* were the most frequent species. In the Grassland Biome, *O. ficus-indica* and *Rosa eglanteria* were the most frequent invaders. In the Savanna Biome, *O. ficus-indica* was the most frequent invader.

Prominence

Opuntia ficus-indica scored the highest prominence value of 58.4 in the study area. The next most prominent species were *Acacia mearnsii* (20.8) and *A. cyclops* (15.2) (Table 9).

In the Fynbos Biome, *Acacia mearnsii, A. saligna, A. cyclops* and *Pinus pinaster* were the most prominent species. In the Nama-Karoo Biome, *Opuntia ficus-indica* was the most prominent species followed by *O.* cf. *robusta* cultivars and *Agave americana*.

In the Grassland Biome, *Rosa eglanteria, Acacia mearnsii* and *Opuntia ficus-indica* were the most prominent invaders. In the Savanna Biome, *O. ficus-indica* was by far the most prominent invader followed by *A. cyclops* and *A. mearnsii*.

Acacia dealbata and *Rubus affinis* deserve mention as the second and third most prominent invaders after *A. mearnsii* in moist subtropical grassland. *Psidium guajava* was ranked fourth in coastal 'forest' after *A. cyclops, A. mearnsii* and *Opuntia ficus-indica. A. longifolia* and *Hakea sericea* were abundant in places within mountain fynbos.

Patterns of invasion

Alien plant invasion was recorded in streambank, roadside and veld habitats throughout the eastern Cape (Figures 4 & 5). However, most invasion in terms of species

TABLE 6.—Alien species occurring in streambank habitats of the Nama-Karoo Biome

Veld type category	False karoo			Karoo			Total		
No. watercourse crossings	131			45			176		
	F	I	P	F	I	P	F	I	P
Acacia dealbata	0.8		1.6				0.6		1.4
Agave americana	4.6		9.4	8.9		**34.8**	5.7		**13.1**
Arundo donax	6.1		**12.5**	2.2		8.7	5.1		**11.8**
Atriplex sp. cf. *nummularia*				11.1		**43.5**	2.8		6.5
Cupressus arizonica	0.8		1.6				0.6		1.4
Eucalyptus sp. cf. *camaldulensis*				2.2		8.7	0.6		1.4
Eucalyptus spp.	6.9		**14.1**				5.1		**11.8**
Gleditsia triacanthos	1.5		3.1				1.1		2.6
Melia azedarach				2.2		8.7	0.6		1.4
Nicotiana glauca	5.3		**10.9**	8.9		**34.8**	6.3		**14.5**
Opuntia ficus-indica	5.3		**10.9**				4.0		**9.2**
Opuntia sp. cf. *robusta*	0.8		1.6				0.6		1.4
Populus × *canescens*	5.3		**13.3**				4.0		**11.3**
Populus sp. cf. *deltoides*	2.3		4.7				1.7		3.9
Populus sp. cf. *nigra*	6.1		**12.5**				4.5		**10.4**
Prosopis sp.				2.2		8.7	0.6		1.4
Prunus persica	0.8		1.6				0.6		1.4
Ricinus communis	1.5		3.1	2.2		8.7	1.7		3.9
Robinia pseudoacacia	1.5		3.1				1.1		2.6
Salix babylonica	17.6	1.5	**69.8**				13.1	1.1	**60.0**
Schinus molle	9.9		**20.2**	2.2		8.7	8.0		**18.4**
Sesbania punicea	*						*		
Tamarix sp. cf. *ramosissima*	2.3		4.7	8.9		**34.8**	4.0		**9.2**
Yucca sp. cf. *aloifolia*	0.8		1.6				0.6		1.4

F = % frequency of occurrence; I = % crossings heavily invaded; P = prominence value; * species occurring in the given category but not included in a formal recording at a watercourse crossing; bold numbers = the highest prominence values in a given category which add up to ± 80% of the summed prominence values (see text).

diversity and abundance of invaders was recorded in the wetter eastern parts. In roadside and veld habitats invasion was most severe in the districts of Port Elizabeth, Uitenhage, Grahamstown, East London, Hogsback (Amatole Mountains) and Stutterheim (Figures 5 & 6). Invasion was less, but still considerable, in the high altitude grassland areas of Barkly East and Maclear.

A comparison of Figures 4 and 5 shows that similar patterns of invasion were recorded in streambank, roadside and veld habitats, except that in the western dry mountain areas there was more severe invasion of the streambank habitat than of roadside and veld habitats. This pattern of streambank invasion in the dry mountain areas was almost entirely due to *Populus* × *canescens* (Figure 8C) and *Salix babylonica* (Figure 8K).

DISCUSSION

Prominent and potentially important species

Several *Opuntia* species have been, or still are, troublesome invaders in the eastern Cape. *O. vulgaris* was a major weed at the end of the nineteenth century but today is of minor importance following a very successful biological control programme (Zimmermann *et al.* 1986). Species infesting large areas at present are *O. ficus-indica* and

TABLE 7.—Alien species occurring in streambank habitats of the Grassland, Savanna and Fynbos Biomes and the study area

Biome and veld type category	Grassland Biome									Savanna Biome									Fynbos Biome			Total study area		
	Temperate grassland			Moist subtropical grassland			Total			Coastal 'forest'			Subtropical thicket & savanna			Total			Mountain fynbos					
No. watercourse crossings	188			27			215			56			175			231			16			638		
	F	I	P	F	I	P	F	I	P	F	I	P	F	I	P	F	I	P	F	I	P	F	I	P
Acacia																								
cyclops										37.5		**37.2**	2.3		2.6	10.8		**14.1**	12.5		6.5	4.2		**4.4**
dealbata	2.7	1.1	6.7	25.9	11.1	**28.5**	5.6	2.3	**11.7**													2.0	0.8	**6.2**
longifolia										3.6	1.8	**15.2**				0.9	0.4	**4.8**	6.3		3.8	0.5	0.2	1.3
mearnsii	2.1	1.1	4.8	25.9	18.5	**57.4**	5.1	3.3	**17.8**	23.2		**19.9**	9.1	0.6	**22.1**	12.6	0.4	**21.6**	75.0	62.5	**115.8**	8.2	2.8	**32.2**
melanoxylon				*			*															*		
saligna										5.4		3.8	0.6		0.7	1.7		1.7	37.5		20.0	1.6		1.6
Agave																								
americana	3.2		2.8				2.8		2.2				1.1		1.3	0.9		0.9	*			2.8		2.7
Ailanthus																								
altissima	*						*															*		
Arundo																								
donax	1.6		1.3				1.4		1.0	1.8		1.3	13.7	1.1	**33.0**	10.8	0.9	**22.7**	6.3		3.3	6.0	0.3	**7.6**
Atriplex																								
sp. cf. *nummularia*													2.3		2.6	1.7		1.7				1.4		1.3
Bambusa																								
sp. cf. *balcooa*										*			*			*						*		
Caesalpinia																								
gilliesii													0.6		0.7	0.4		0.4				0.2		0.2
Cardiospermum																								
sp.										1.8		1.3	0.6		0.7	0.9		0.9				0.3		0.3
Casuarina																								
cunninghamiana													2.3		2.6	1.7		1.7				0.6		0.6
sp.													0.6		0.7	0.4		0.4				0.2		0.2
Cestrum																								
laevigatum										10.7		**7.5**	1.1		1.3	3.5		3.4				1.3		1.2
Cortaderia																								
sp.																			*			*		
Cupressus																								
arizonica	0.5		0.4				0.5		0.4													0.3		0.3
Cydonia																								
oblonga	*						*															*		
Eucalyptus																								
sp. cf. *camaldulensis*	0.5		0.4				0.5		0.4				1.1		1.3	0.9		0.9				0.6		0.6
spp.	1.1		0.9	*			0.9		0.7	5.4		5.6	7.4		**9.3**	6.9		**8.0**	18.8	6.3	13.9	4.7	0.2	**5.3**
Gleditsia																								
triacanthos	*						*															0.3		0.3

F = % frequency of occurrence; I = % crossings heavily invaded; P = prominence value; * species occurring in the given category but not included in a formal recording at a watercourse crossing; bold numbers = the highest prominence values in a given category which add up to ± 80% of the summed prominence values (see text).

TABLE 7.—Alien species occurring in streambank habitats of the Grassland, Savanna and Fynbos Biomes and the study area (continued)

Biome and veld type category	Grassland Biome									Savanna Biome									Fynbos Biome					
	Temperate grassland			Moist subtropical grassland			Total			Coastal 'forest'			Subtropical thicket & savanna			Total			Mountain fynbos			Total study area		
No. watercourse crossings	188			27			215			56			175			231			16			638		
	F	I	P	F	I	P	F	I	P	F	I	P	F	I	P	F	I	P	F	I	P	F	I	P
Ipomoea sp. cf. *purpurea*													0.6		0.7	0.4		0.4				0.2		0.2
Jacaranda mimosifolia										*						*						*		
Lantana camara										8.9		**6.2**	1.7		2.8	3.5		4.0				1.3		1.3
Ligustrum sinense				3.7		1.8	0.5		0.4													0.2		0.2
?*Ligustrum* sp.				3.7	3.7	5.8	0.5	0.5	1.4													0.2	0.2	0.8
Melia azedarach										8.9		**6.2**	5.1		**5.8**	6.1		**6.0**	*			2.4		2.2
Morus alba	0.5		0.4				0.5		0.4													0.2		0.2
Nerium oleander	0.5		0.4				0.5		0.4				6.9		**7.8**	5.2		**5.1**				2.0		1.8
Nicotiana glauca	2.7		2.2				2.3		1.7	1.8		1.3	14.3		**17.1**	11.3		**11.7**				6.6		**6.1**
Opuntia ficus-indica	2.7		2.2				2.3		1.7	7.1		5.0	8.0		**9.9**	7.8		**8.3**	*			4.7		**4.4**
Opuntia vulgaris										7.1		5.0	1.1		1.3	2.6		2.6				0.9		0.8
Opuntia sp. cf. *robusta*	0.5		0.4				0.5		0.4													0.3		0.3
Paraserianthes lophantha										3.6		2.5				0.9		0.9				0.3		0.3
Passiflora caerulea										1.8		1.3				0.4		0.4				0.2		0.2
Pennisetum purpureum										1.8		1.3				0.4		0.4				0.2		0.2
Phoenix sp. cf. *dactylifera*													0.6		0.7	0.4		0.4				0.2		0.2
Phytolacca dioica													0.6		0.7	0.4		0.4	*			0.2		0.2
Pinus halepensis	*						*			1.8		1.3	0.6		0.7	0.9		0.9	*			0.3		0.3
Pinus patula				*			*															*		
Pinus pinaster																			*			*		
Pinus radiata				*			*															*		

F = % frequency of occurrence; I = % crossings heavily invaded; P = prominence value; * species occurring in the given category but not included in a formal recording at a watercourse crossing; bold numbers = the highest prominence values in a given category which add up to ± 80% of the summed prominence values (see text).

TABLE 7.—Alien species occurring in streambank habitats of the Grassland, Savanna and Fynbos Biomes and the study area (continued)

Biome and veld type category	Grassland Biome									Savanna Biome									Fynbos Biome					
	Temperate grassland			Moist subtropical grassland			Total			Coastal 'forest'			Subtropical thicket & savanna			Total			Mountain fynbos			Total study area		
No. watercourse crossings	188			27			215			56			175			231			16			638		
	F	I	P	F	I	P	F	I	P	F	I	P	F	I	P	F	I	P	F	I	P	F	I	P
Populus																								
× *canescens*	28.2	6.4	**54.7**	25.9	7.4	**21.6**	27.9	6.5	**46.6**	3.6		2.5	0.6		0.7	1.3		1.3	31.3	12.5	**30.1**	11.8	2.5	**28.7**
sp. cf. *deltoides*	1.6		1.3	3.7		1.8	1.9		1.4													1.1		1.0
sp. cf. *nigra*	8.5		**7.0**	7.4		3.5	8.4		6.3													4.1		3.8
Prosopis																								
sp.																						0.2		0.2
Prunus																								
armeniaca	0.5		0.4				0.5		0.4													0.2		0.2
persica	3.2		2.6	18.5		8.8	5.1		3.7	1.8		1.3				0.4		0.4				2.0		1.8
Psidium																								
guajava										8.9		**6.2**	1.1		1.3	3.0		3.0				1.1		1.0
Pyracantha																								
angustifolia	2.7		2.2	3.7		1.8	2.8		2.1													0.9		0.8
Quercus																								
robur				3.7		1.8	0.5		0.4	*						*			*			0.2		0.2
Ricinus																								
communis										41.1		**28.8**	16.6		**18.9**	22.5		**22.2**				8.6		**7.8**
Robinia																								
pseudoacacia	2.7		2.9	3.7		2.4	2.8		2.7													1.3		1.6
Rosa																								
eglanteria	9.6		**7.7**	3.7		1.8	8.8		6.4				0.6		0.7	0.4		0.4				3.1		2.8
Rubus																								
affinis				3.7		1.8	0.5		0.4													0.2		0.2
Salix																								
babylonica	41.0	4.8	**51.8**	66.7	3.7	**36.9**	44.2	4.7	**47.8**				3.4		3.9	2.6		2.6	6.3		3.3	19.6	1.9	**28.2**
caprea	0.5		0.4	14.8		7.0	2.3		1.7													0.8		0.7
fragilis	21.8	4.8	**41.2**	14.8	3.7	**15.9**	20.9	4.7	**35.2**													7.1	1.6	**18.0**
Sambucus																								
sp.	*						*															*		
Schinus																								
molle	5.9		4.7				5.1		3.7				5.1		**5.8**	3.9		3.9	*			5.3		**4.8**
Senna																								
didymobotrya													0.6		0.7	0.4		0.4				0.2		0.2
septemtrionalis													0.6		0.7	0.4		0.4				0.2		0.2
?*Senna*																								
sp.																			6.3		3.3	0.2		0.2
Sesbania																								
punicea				3.7		1.8	0.5		0.4	17.9	1.8	27.0	9.1	1.1	**31.3**	11.3	1.3	**30.1**				4.2	0.5	7.2

F = % frequency of occurrence; I = % crossings heavily invaded; P = prominence value; * species occurring in the given category but not included in a formal recording at a watercourse crossing; bold numbers = the highest prominence values in a given category which add up to ± 80% of the summed prominence values (see text).

TABLE 7.—Alien species occurring in streambank habitats of the Grassland, Savanna and Fynbos Biomes and the study area (continued)

Biome and veld type category	Grassland Biome: Temperate grassland			Grassland Biome: Moist subtropical grassland			Grassland Biome: Total			Savanna Biome: Coastal 'forest'			Savanna Biome: Subtropical thicket & savanna			Savanna Biome: Total			Fynbos Biome: Mountain fynbos			Total study area		
No. watercourse crossings	188			27			215			56			175			231			16			638		
	F	I	P	F	I	P	F	I	P	F	I	P	F	I	P	F	I	P	F	I	P	F	I	P
Solanum																								
hispidum										10.7		**7.5**	2.9		3.3	4.8		**4.7**				1.7		1.6
mauritianum										7.1		5.0	2.3		3.4	3.5		4.0	*			1.3		1.3
seaforthianum													0.6		0.7	0.4		0.4				0.2		0.2
Tamarix																								
sp. cf. *ramosissima*													1.7		1.9	1.3		1.3				1.6		1.5
Ulmus																								
sp.	0.5		0.4				0.5		0.4													0.2		0.2
Washingtonia																								
sp.													0.6		0.7	0.4		0.4				0.2		0.2
Yucca																								
sp. cf. *aloifolia*	*						*															0.2		2.0

F = % frequency of occurrence; I = % crossings heavily invaded; P = prominence value; * species occurring in the given category but not included in a formal recording at a watercourse crossing; bold numbers = the highest prominence values in a given category which add up to ± 80% of the summed prominence values (see text).

TABLE 8.—Alien species occurring in roadside and veld habitats of the Nama-Karoo Biome

Veld type category	False karoo			Karoo			Total		
No. road transects	66			28			94		
	F	A	P	F	A	P	F	A	P
Agave									
americana	42.4	2.0	**21.9**	39.3	2.0	**25.3**	41.5	2.0	**22.7**
Arundo									
donax	3.0	1.0	1.3				2.1	1.0	0.9
Atriplex									
sp. cf. nummularia	10.6	2.0	5.6	42.9	2.0	**27.0**	20.2	2.0	**11.4**
Caesalpinia									
gilliesii	*						*		
Cupressus									
arizonica	1.5	1.0	0.6				1.1	1.0	0.5
Eucalyptus									
spp.	6.1	2.0	3.3				4.3	2.0	2.4
Gleditsia									
triacanthos	10.6	1.0	4.8				7.4	1.0	3.5
Melia									
azedarach	*			*			*		
Nicotiana									
glauca	10.6	1.0	5.1	39.3	3.0	**40.6**	19.1	3.0	**14.4**
Opuntia									
ficus-indica	78.8	3.0	**90.0**	85.7	3.0	**69.2**	80.9	3.0	**84.8**
imbricata	1.5	2.0	0.8				1.1	2.0	0.6
lindheimeri	1.5	2.0	0.8				1.1	2.0	0.6
sp. cf. *robusta*	65.2	2.0	**35.5**	46.4	2.0	**25.5**	59.6	2.0	**32.8**
Parkinsonia									
aculeata	*						*		
Pinus									
halepensis	1.5	2.0	0.8				1.1	2.0	0.6
Populus									
× *canescens*	*						*		
sp. cf. *deltoides*	1.5	1.0	0.6				1.1	1.0	0.5
sp. cf. *nigra*	*						*		
Prosopis									
spp.	9.1	1.0	4.0	14.3	2.0	8.7	10.6	2.0	5.3
Prunus									
armeniaca	*						*		
persica	7.6	1.0	3.4				5.3	1.0	2.4
Pyracantha									
angustifolia	6.1	1.0	2.7				4.3	1.0	2.0
Ricinus									
communis	*			3.6	1.0	1.7	1.1	1.0	0.5
Robinia									
pseudoacacia	1.5	1.0	0.6				1.1	1.0	0.5
Rosa									
eglanteria	1.5	2.0	0.8				1.1	2.0	0.6
Schinus									
molle	24.2	2.0	**12.8**				17.0	2.0	9.3
Tamarix									
sp. cf. ramosissima	3.0	1.0	1.3				2.1	1.0	0.9
Trichocereus									
sp. cf. *spachianus*	6.1	1.0	2.6	3.6	2.0	2.1	5.3	1.0	2.4
Ulmus									
spp.	1.5	2.0	0.8				1.1	2.0	0.6

F = % frequency of occurrence; A = mean abundance rating; P = prominence value; * species occurring in the given category but not included in a formal recording in a road transect; bold numbers = the highest prominence values in a given category which add up to ± 80% of the summed prominence values (see text).

O. aurantiaca (Zimmermann *et al.* 1986). The latter species, known as jointed cactus, is an inconspicuous low-growing species and was excluded from this survey because it was easily overlooked.

Opuntia ficus-indica (Figure 7N) has been naturalized in the eastern Cape for more than 200 years. According to MacDonald (1891) it was first introduced to this region in 1750. Although it was found growing wild between 1772 and 1775 it seems that until at least 1834 it remained largely within the confines of cultivation. By 1859 it had infested a few farms. Thereafter it spread rapidly and by 1891 it had infested 282 000 ha of land in the districts of Graaff-Reinet, Aberdeen, Jansenville, Somerset East and Willowmore. Localized infestations were found in many other districts. By 1932, prior to a biological control campaign, it occurred on 800 000 ha of land in the Cape Province; 400 000 ha in the eastern Cape and Karoo were densely infested (Stirton 1978).

Cochineal (*Dactylopius opuntiae*) aided by felling, caused the collapse of 80% of the 400 000 ha of dense infestations (Stirton 1978). The moth *Cactoblastis cactorum* was effective in killing a substantial proportion of the

TABLE 9.—Alien species occurring in roadside and veld habitats of the Grassland, Savanna and Fynbos Biomes and the study area

Biome and veld type category	Grassland Biome: Temperate grassland			Grassland Biome: Moist subtropical grassland			Grassland Biome: Total			Savanna Biome: Coastal 'forest'			Savanna Biome: Subtropical thicket & savanna			Savanna Biome: Total			Fynbos Biome: Mountain fynbos			Total study area		
No. road transects	98			30			128			62			85			147			15			384		
	F	A	P	F	A	P	F	A	P	F	A	P	F	A	P	F	A	P	F	A	P	F	A	P
Acacia																								
baileyana	2.0	2.0	0.9	10.0	1.0	2.7	3.9	1.0	1.5	1.6	1.0	0.5				0.7	1.0	0.2	*			3.4	1.0	1.1
cyclops										40.3	5.0	**47.3**	7.1	4.0	6.5	21.1	5.0	**23.7**	66.7	4.0	**27.2**	10.7	5.0	**15.2**
dealbata	1.0	1.0	0.4	26.7	4.0	**21.1**	7.0	4.0	**9.2**				1.2	2.0	0.4	0.7	2.0	0.2				2.6	4.0	2.4
decurrens				3.3	3.0	1.1	0.8	3.0	0.4													0.3	3.0	0.1
longifolia										4.8	2.0	1.4	*			2.0	2.0	0.6	33.3	5.0	**14.9**	2.1	4.0	1.9
mearnsii	5.1	3.0	4.3	70.0	5.0	**66.9**	20.3	4.0	**31.5**	56.5	4.0	**33.3**	4.7	2.0	1.7	26.5	4.0	**15.4**	86.7	5.0	**48.6**	20.3	4.0	**20.8**
melanoxylon	3.1	1.0	1.4	26.7	3.0	**9.3**	8.6	3.0	4.3	4.8	1.0	1.4	1.2	1.0	0.4	2.7	1.0	0.8	*			3.9	3.0	1.6
pycnantha										1.6	2.0	0.5				0.7	2.0	0.2				0.3	2.0	0.1
saligna										19.4	4.0	**10.9**	*			8.2	4.0	**4.7**	40.0	6.0	**32.4**	4.7	5.0	**6.4**
Agave																								
americana	27.6	2.0	**12.4**	*			21.1	2.0	**8.0**	*			48.2	2.0	**17.4**	27.9	2.0	**9.4**	13.3	2.0	2.9	28.4	2.0	**10.4**
sisalana										6.5	2.0	1.9	2.4	1.0	0.8	4.1	2.0	1.3				1.6	2.0	0.6
sp.										*						*						*		
Ailanthus																								
altissima																			*			*		
Arundo																								
donax										*			7.1	1.0	2.4	4.1	1.0	1.3				2.1	1.0	0.7
Atriplex																								
sp. cf. *nummularia*	1.0	1.0	0.4				0.8	1.0	0.3				8.2	2.0	2.9	4.8	2.0	1.6				6.3	2.0	2.3
Bambuseae																								
sp.										*						*						*		
Caesalpinia																								
decapetala	1.0	2.0	0.4				0.8	2.0	0.3													0.3	2.0	0.1
gilliesii																						*		
Casuarina																								
cunninghamiana													1.2	4.0	0.6	0.7	4.0	0.3				0.3	4.0	0.2
sp.				*			*			*						*			6.7	2.0	1.4	0.3	2.0	0.1
Cereus																								
peruvianus	*						*			1.6	2.0	0.5	4.7	1.0	1.6	3.4	1.0	1.1				1.3	1.0	0.4
Cestrum																								
laevigatum										4.8	2.0	1.4	*			2.0	2.0	0.6				0.8	2.0	0.3
Cortaderia																								
sp.				6.7	1.0	1.7	1.6	1.0	0.6	*						*			*			0.5	1.0	0.2
Cotoneaster																								
sp.				6.7	2.0	1.8	1.6	2.0	0.6													0.5	2.0	0.2
Crotalaria																								
sp.										1.6	2.0	0.5				0.7	2.0	0.2				0.3	2.0	0.1

F = % frequency of occurrence; A = mean abundance rating; P = prominence value; * species occurring in the given category but not included in a formal recording in a road transect; bold numbers = the highest prominence values in a given category which add up to ± 80% of the summed prominence values (see text).

TABLE 9.—Alien species occurring in roadside and veld habitats of the Grassland, Savanna and Fynbos Biomes and the study area (continued)

Biome and veld type category	Grassland Biome: Temperate grassland			Grassland Biome: Moist subtropical grassland			Grassland Biome: Total			Savanna Biome: Coastal 'forest'			Savanna Biome: Subtropical thicket & savanna			Savanna Biome: Total			Fynbos Biome: Mountain fynbos			Total study area		
No. road transects	98			30			128			62			85			147			15			384		
	F	A	P	F	A	P	F	A	P	F	A	P	F	A	P	F	A	P	F	A	P	F	A	P
Cupressus arizonica	10.2	1.0	4.5	*			7.8	1.0	2.9													2.9	1.0	1.0
?Cupressus sp.	2.0	1.0	0.9				1.6	1.0	0.6													0.5	1.0	0.2
Cydonia oblonga				*			*															*		
Eucalyptus																								
cladocalyx																			6.7	2.0	1.4	0.3	2.0	0.1
diversicolor																			*			*		
ficifolia										*						*						*		
lehmannii										11.3	2.0	3.2				4.8	2.0	1.5	6.7	3.0	1.5	2.1	2.0	0.7
spp.	10.2	1.0	4.3	30.0	3.0	**8.9**	14.8	2.0	**5.9**	27.4	3.0	**9.1**	2.4	1.0	0.8	12.9	3.0	4.6	60.0	3.0	**14.4**	13.3	2.0	**5.3**
Ficus carica				*			*															*		
?Ficus sp.													1.2	2.0	0.4	0.7	2.0	0.2				0.3	2.0	0.1
Fraxinus sp. cf. *americana*	2.0	2.0	1.1				1.6	2.0	0.7													0.5	2.0	0.2
Gleditsia triacanthos	1.0	2.0	0.5				0.8	2.0	0.3													2.1	1.0	0.7
Hakea sericea																			6.7	5.0	2.5	0.3	5.0	0.3
?Hylocereus sp.										*			*			*						*		
Jacaranda mimosifolia										*			*			*						*		
?Juniperus sp.	1.0	1.0	0.4				0.8	1.0	0.3													0.3	1.0	0.1
?Lagerstroemia indica										*						*						*		
Lantana camara										16.1	4.0	**10.8**	3.5	2.0	1.3	8.8	4.0	**5.4**	*			3.4	4.0	2.6
Leptospermum laevigatum										1.6	3.0	0.6				0.7	3.0	0.3	6.7	2.0	1.4	0.5	3.0	0.2
Ligustrum sinense	*			6.7	2.0	1.8	1.6	2.0	0.6													0.5	2.0	0.2
Melia azedarach										9.7	2.0	2.9	10.6	2.0	3.6	10.2	2.0	3.3	6.7	2.0	1.4	4.2	2.0	1.5

F = % frequency of occurrence; A = mean abundance rating; P = prominence value; * species occurring in the given category but not included in a formal recording in a road transect; bold numbers = the highest prominence values in a given category which add up to ± 80% of the summed prominence values (see text).

TABLE 9.—Alien species occurring in roadside and veld habitats of the Grassland, Savanna and Fynbos Biomes and the study area (continued)

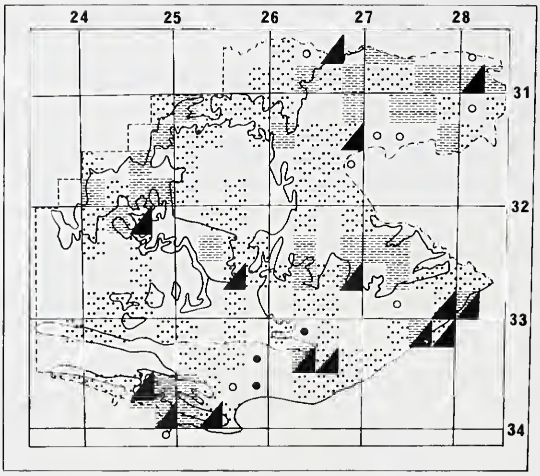
Biome and veld type category	Grassland Biome: Temperate grassland			Grassland Biome: Moist subtropical grassland			Grassland Biome: Total			Savanna Biome: Coastal 'forest'			Savanna Biome: Subtropical thicket & savanna			Savanna Biome: Total			Fynbos Biome: Mountain fynbos			Total study area		
No. road transects	98			30			128			62			85			147			15			384		
	F	A	P	F	A	P	F	A	P	F	A	P	F	A	P	F	A	P	F	A	P	F	A	P
Nerium																								
oleander													1.2	2.0	0.4	0.7	2.0	0.2				0.3	2.0	0.1
Nicotiana																								
glauca	4.1	2.0	1.9				3.1	2.0	1.2	4.8	2.0	1.4	38.8	2.0	**14.9**	24.5	2.0	**8.7**				15.1	2.0	**6.1**
Opuntia																								
ficus-indica	61.2	3.0	**47.8**	23.3	2.0	**6.7**	52.3	3.0	**30.9**	40.3	4.0	**19.3**	97.6	5.0	**116.2**	73.5	5.0	**75.3**	53.3	3.0	12.5	67.4	4.0	**58.4**
imbricata	2.0	2.0	0.9				1.6	2.0	0.6				*			*						0.8	2.0	0.3
lindheimeri													2.4	3.0	1.0	1.4	3.0	0.5				0.8	3.0	0.3
stricta	*			3.3	2.0	0.9	0.8	2.0	0.3				2.4	3.0	1.2	1.4	3.0	0.7				0.5	3.0	0.3
vulgaris										8.1	3.0	3.0	3.5	2.0	1.3	5.4	3.0	2.0				2.1	3.0	0.9
sp. cf. *robusta*	34.7	2.0	**15.6**				26.6	2.0	**10.2**				15.3	1.0	5.2	8.8	1.0	2.8				26.8	2.0	**9.6**
Paraserianthes																								
lophantha										*						*			6.7	1.0	1.4	0.3	1.0	0.1
Parkinsonia																								
aculeata																						*		
Passiflora																								
caerulea										*			1.2	1.0	0.4	0.7	1.0	0.2	*			0.3	2.0	0.1
Pennisetum																								
purpureum										1.6	5.0	1.2				0.7	5.0	0.5				0.3	5.0	0.3
Phytolacca																								
dioica													4.7	3.0	1.8	2.7	3.0	1.0				1.0	3.0	0.4
Pinus																								
?elliottii	1.0	1.0	0.4				0.8	1.0	0.3													0.3	1.0	0.1
halepensis	8.2	3.0	**6.3**	20.0	2.0	5.3	10.9	3.0	**5.5**	22.6	3.0	8.9	1.2	1.0	0.4	10.2	3.0	4.2	46.7	3.0	10.3	9.6	3.0	**4.3**
patula				13.3	4.0	**6.9**	3.1	4.0	2.7	*						*						1.0	4.0	0.7
pinaster										3.2	2.0	0.9				1.4	2.0	0.4	46.7	5.0	**22.0**	2.3	5.0	2.6
pinea	*			10.0	2.0	2.6	2.3	2.0	0.9													0.8	2.0	0.3
radiata				6.7	3.0	3.5	1.6	3.0	1.0	1.6	1.0	0.5				0.7	1.0	0.2	6.7	3.0	1.5	0.8	3.0	0.4
roxburghii	*						*															*		
spp.	1.0	2.0	0.4	10.0	3.0	2.9	3.1	2.0	1.3	4.8	2.0	1.5	*			2.0	2.0	0.7	6.7	2.0	1.4	0.8	2.0	0.4
Populus																								
× *canescens*	5.1	1.0	2.3	3.3	1.0	0.8	4.7	1.0	1.8				*			*			*			1.6	1.0	0.6
sp. cf. *deltoides*	1.0	1.0	0.4				0.8	1.0	0.3													0.5	1.0	0.2
sp. cf. *nigra*	1.0	2.0	0.5	3.3	1.0	0.8	1.6	2.0	0.6													0.5	2.0	0.2
Prosopis																								
spp.													*			*						2.6	2.0	0.9
Prunus																								
armeniaca	4.1	1.0	1.7				3.1	1.0	1.1													1.0	1.0	0.3

F = % frequency of occurrence; A = mean abundance rating; P = prominence value; * species occurring in the given category but not included in a formal recording in a road transect; bold numbers = the highest prominence values in a given category which add up to ± 80% of the summed prominence values (see text).

TABLE 9.—Alien species occurring in roadside and veld habitats of the Grassland, Savanna and Fynbos Biomes and the study area (continued)

Biome and veld type category	Grassland Biome: Temperate grassland			Grassland Biome: Moist subtropical grassland			Grassland Biome: Total			Savanna Biome: Coastal 'forest'			Savanna Biome: Subtropical thicket & savanna			Savanna Biome: Total			Fynbos Biome: Mountain fynbos			Total study area		
No. road transects	98			30			128			62			85			147			15			384		
	F	A	P	F	A	P	F	A	P	F	A	P	F	A	P	F	A	P	F	A	P	F	A	P
Prunus persica	25.5	3.0	**16.2**	40.0	2.0	**10.7**	28.9	2.0	**13.5**	*			2.4	2.0	0.9	1.4	2.0	0.5	6.7	1.0	1.4	11.7	2.0	**4.7**
Psidium guajava										24.2	5.0	**17.9**	*			10.2	5.0	**7.7**	*			3.9	5.0	**3.9**
Pyracantha angustifolia	4.1	1.0	1.7	13.3	2.0	3.7	6.3	1.0	2.4													3.1	1.0	1.1
?crenulata	1.0	1.0	0.4				0.8	1.0	0.3													0.3	1.0	0.1
Quercus robur				6.7	1.0	1.7	1.6	1.0	0.6													0.5	1.0	0.2
Ricinus communis				3.3	2.0	0.9	0.8	2.0	0.3	33.9	3.0	**12.1**	30.6	2.0	**11.3**	32.0	3.0	**11.6**				12.8	3.0	**5.2**
Robinia pseudoacacia	5.1	1.0	2.1	6.7	1.0	1.8	5.5	1.0	2.0													2.1	1.0	0.7
Rosa eglanteria	41.8	4.0	**64.6**	30.0	3.0	**10.2**	39.1	4.0	**40.2**				*			*			*			13.3	4.0	**10.4**
Rubus affinis	*			16.7	5.0	**16.6**	3.9	5.0	**7.2**													1.3	5.0	1.7
sp.				6.7	3.0	3.0	1.6	3.0	1.2	1.6	1.0	0.5				0.7	1.0	0.2				0.8	3.0	0.4
Salix sp. cf. *caprea*				3.3	1.0	0.8	0.8	1.0	0.3													0.3	2.0	0.1
Sambucus sp.	1.0	1.0	0.4	*			0.8	1.0	0.3													0.3	1.0	0.1
Schinus molle	10.2	1.0	4.2	*			7.8	1.0	2.8	*			4.7	2.0	1.6	2.7	2.0	0.9				7.8	2.0	2.8
Senna didymobotrya										1.6	2.0	0.5	*			0.7	2.0	0.2				0.3	2.0	0.1
septemtrionalis										*						*						*		
?Senna sp.										*						*						*		
Sesbania punicea				*			*			6.5	2.0	1.9	1.2	2.0	0.4	3.4	2.0	1.1	*			1.3	2.0	0.4
Solanum hispidum										4.8	3.0	1.5	*			2.0	3.0	0.7				0.8	3.0	0.3
mauritianum				16.7	3.0	5.0	3.9	3.0	0.6	9.7	3.0	3.0	2.4	2.0	0.8	5.4	3.0	1.8	*			3.4	3.0	1.3
Tamarix sp. cf. *ramosissima*	1.0	1.0	0.4				0.8	1.0	0.3													0.8	1.0	0.3
Trichocereus sp. cf. *spachianus*	*						*						3.5	3.0	1.6	2.0	3.0	0.9				2.1	2.0	0.8
Ulmus spp.	*			3.3	1.0	0.8	0.8	1.0	0.3													0.5	2.0	0.2

F = % frequency of occurrence; A = mean abundance rating; P = prominence value; * species occurring in the given category but not included in a formal recording in a road transect; bold numbers = the highest prominence values in a given category which add up to ± 80% of the summed prominence values (see text).



1 or more species invasive, but no formal recordings

1 or more species locally abundant

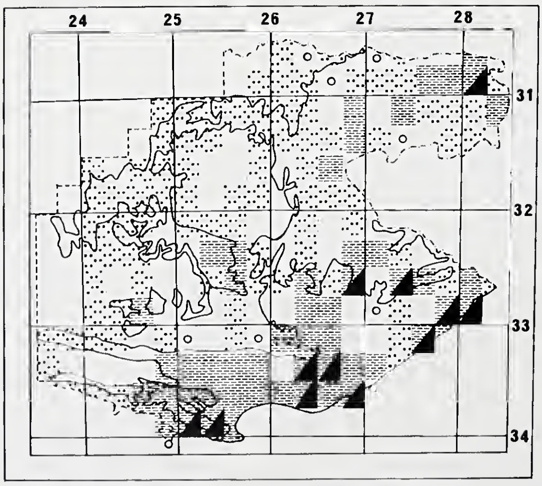
1 or more river crossings invaded

1 or more river crossings heavily invaded

10 or more species per quarter degree square

FIGURE 4.—Invasion in streambank habitats in terms of the intensity of invasion of watercourse crossings and species diversity per quarter degree square.

more isolated plants (Zimmermann *et al.* 1986). The present distribution of *Opuntia ficus-indica* is mainly a reflection of the effects of climate on the insect herbivores, particularly *Dactylopius opuntiae*, and not a direct influence of climate on the plant itself (Zimmermann *et al.* 1986). The insects are most effective under hot and dry conditions and least effective under cool and moist conditions (Zimmermann *et al.* 1986).



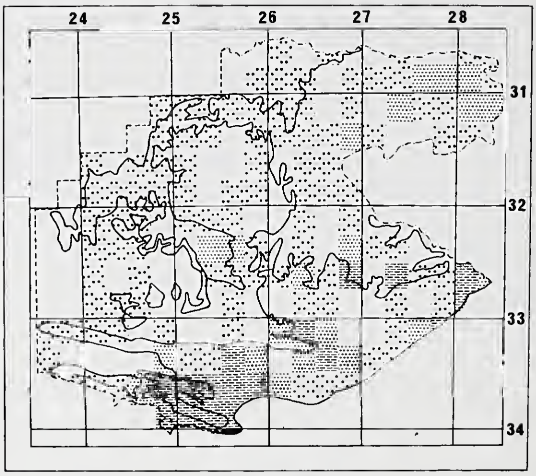
1 or more species invasive, but no formal recordings

1 or more road transects invaded

1 or more road transects heavily invaded

15 or more species per quarter degree square

FIGURE 5.—Invasion in roadside and veld habitats in terms of the intensity of invasion of road transects and species diversity per quarter degree square.



Mean abundance per km:

less than 5 individuals/groups

5–10 11–49 >49

FIGURE 6.—Invasion in roadside and veld habitats in terms of the mean abundance of invaders per kilometre in each quarter degree square.

In this survey the densest populations of *Opuntia ficus-indica* were recorded in the districts of Uitenhage, Port Elizabeth, Addo and Grahamstown (Helspoort and Woodroad Kloof in the Fish River valley). Less dense populations were recorded in the districts of Patensie and Hankey (Gamtoos River valley), Kirkwood, Glenconnor, Kleinpoort (foothills of Kleinwinterhoek and Suurberg ranges), Alexandria, Kenton-on-Sea, Grahamstown (Kariega and Kafferskraal River valleys), Adelaide and Fort Beaufort (Koonap River valley), Seymour, Somerset East and Cradock.

Acacia mearnsii (Figure 7D) was the next most prominent invader after *Opuntia ficus-indica* in roadside and veld habitats and the most prominent species in streambank habitats. It was most abundant in the cool and moist regions which support mountain fynbos and moist subtropical grassland. It was frequently recorded in the warmer coastal lowlands but its average abundance was less than in the previous categories.

Whereas *Opuntia ficus-indica* is being kept in check by its natural insect herbivores, *Acacia mearnsii* has tremendous potential to spread. This is largely due to its ability to produce large quantities of long-lived seeds and the absence of natural seed predators. Seed can remain viable for more than 50 years and over 20 000 seeds per square metre can accumulate under an old tree (Stirton 1978). Seed is very efficiently dispersed by water along watercourses, but judging from the dense stands which develop along roadsides, it can also be dispersed in soil by roadbuilding activities and possibly vehicle tyres. I predict that *Acacia mearnsii* will continue to expand its range and that all the cool and moist mountain regions are particularly susceptible to invasion, as well as all watercourses within the Fynbos, Grassland and Savanna Biomes.

In this survey *Acacia cyclops* (Figure 7A) was found to be restricted to the coastal lowlands and mountains. It was

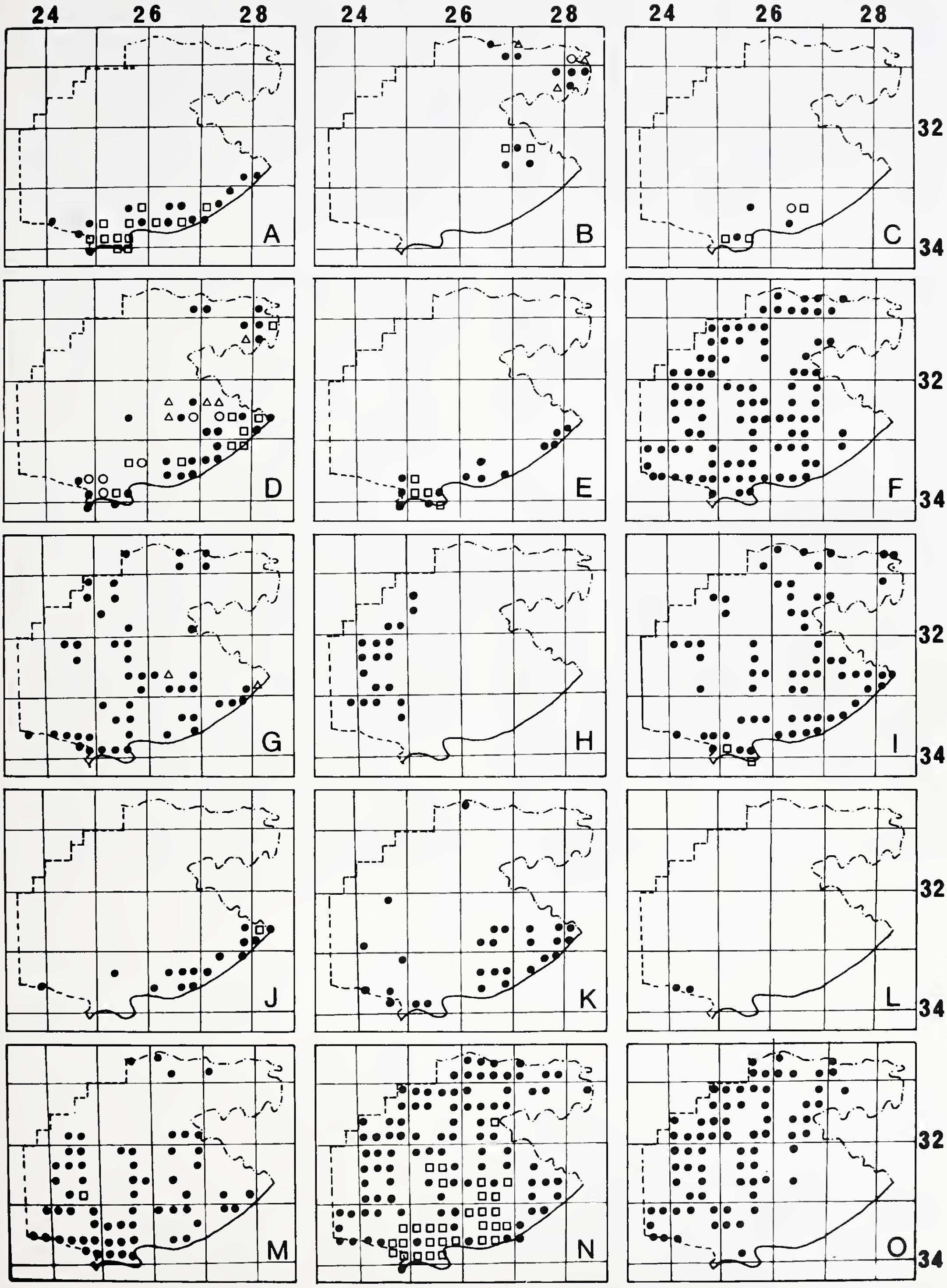


FIGURE 7.—Distribution of the most prominent species: A, *Acacia cyclops*; B, *A. dealbata*; C, *A. longifolia*; D, *A. mearnsii*; E, *A. saligna*; F, *Agave americana*; G, *Arundo donax*; H, *Atriplex* cf. *nummularia*, I, *Eucalyptus* spp.; J, *Lantana camara*; K, *Melia azedarach*; L, *Nerium oleander*; M, *Nicotiana glauca*; N, *Opuntia ficus-indica*; O, *O.* cf. *robusta* cultivars. Highest abundance rating of 4 or less: ●. Highest abundance rating of 5 or more: roadside and veld habitats, □; streambank habitats, △; streambank, roadside and veld habitats, ○.

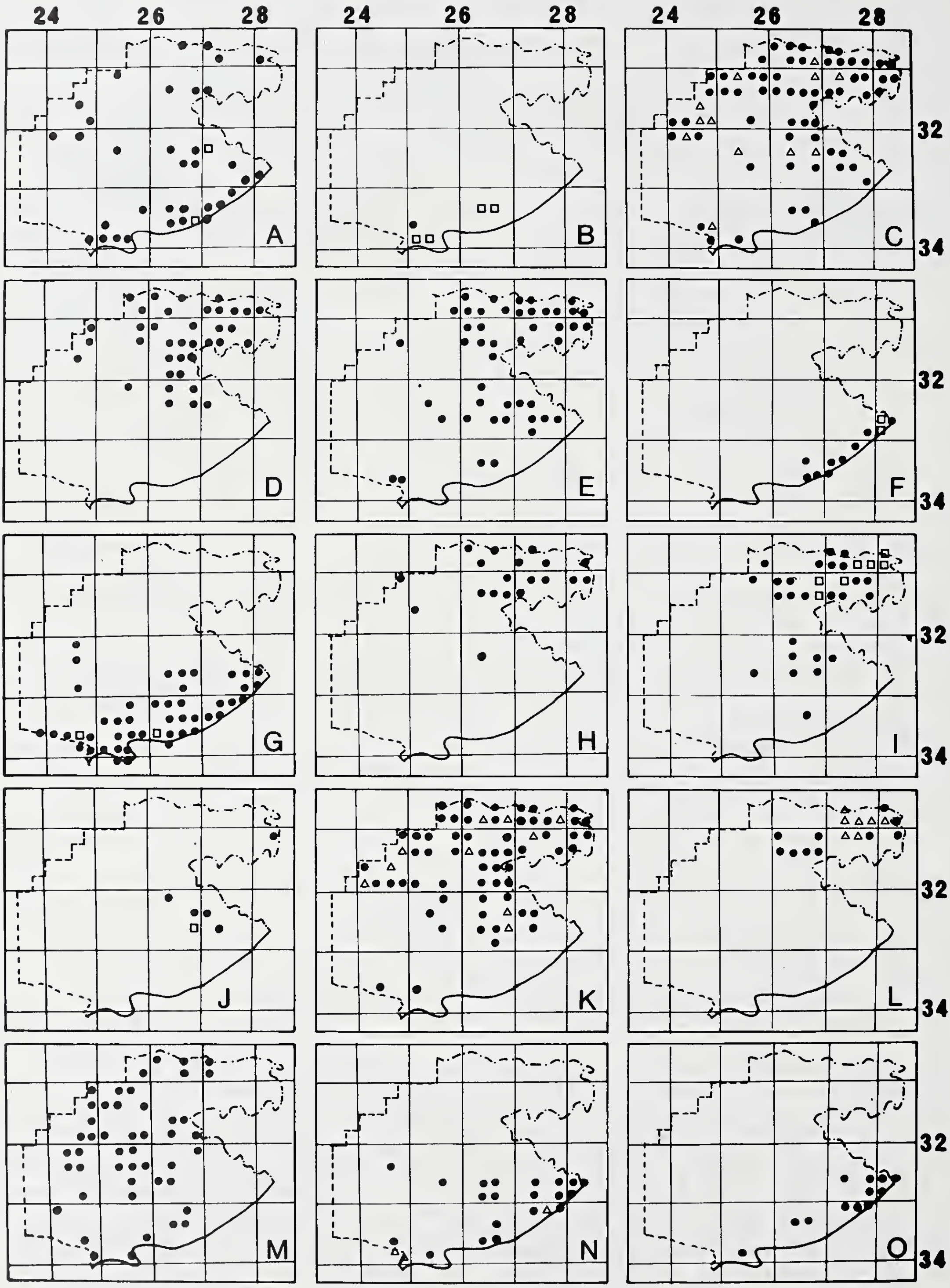


FIGURE 8.—Distribution of the most prominent species: A, *Pinus halepensis*; B, *P. pinaster*; C, *Populus* × *canescens*; D, *Populus* cf. *nigra*; E, *Prunus persica*; F, *Psidium guajava*; G, *Ricinus communis*; H, *Robinia pseudoacacia*; I, *Rosa eglanteria*; J, *Rubus affinis*; K, *Salix babylonica*; L, *S. fragilis*; M, *Schinus molle*; N, *Sesbania punicea*; O, *Solanum mauritianum*. Highest abundance rating of 4 or less: ● Highest abundance rating of 5 or more: roadside and veld habitats, □; streambank habitats, △; streambank, roadside and veld habitats, O.

heavily invasive in parts of coastal 'forest', subtropical thicket and savanna, and mountain fynbos. It was particularly abundant in coastal dune vegetation around Port Elizabeth where it appeared to be the commonest woody species. Its presence in this area dates back to at least the 1890's when it, *A. saligna, A. pycnantha* and *Pinus halepensis* were used in a sand dune reclamation scheme (Stirton 1978). Taylor & Morris (1981) are of the opinion that *A. cyclops* threatens to destroy the structure of indigenous forest precursor communities, grassland and fynbos in coastal vegetation near Port Elizabeth.

Acacia saligna (Figure 7E) had a similar distribution to *A. cyclops*, being restricted to the coastal belt. However, it was only abundant in the Port Elizabeth area in mountain fynbos on the lower slopes of the Vanstadensberg and Elandsberg and in dune vegetation surrounding the airport. It is spreading rapidly in the Grahamstown area and needs to be closely watched (A. Jacot Guillarmod pers. comm.).

Rosa eglanteria (Figure 8I), the sweet brier rose of Europe and Britain, was brought to the eastern Cape by English settlers during the 1820's and shortly afterwards (Palmer 1985). By 1937 it was reported to be a nuisance in the mountainous parts of Barkly East and a possible threat to the indigenous vegetation (National Herbarium, Pretoria). Like many other members of the family Rosaceae it appears to require low winter temperatures to terminate seed dormancy. Its present distribution as a naturalized plant in southern Africa is largely confined to the mountainous districts of Lesotho, Natal, Orange Free State and northeastern Cape (Jacot Guillarmod 1971; National Herbarium, Pretoria). These regions experience the highest frequencies of below-freezing minimum temperatures in southern Africa (Tyson 1986).

This survey showed *Rosa eglanteria* to be heavily invasive in the districts of Barkly East, Rhodes, Naudesnek, Rossouw and Jamestown. It is said to be spreading rapidly in the Rhodes area and that the fruits are eaten by people, Angora goats and birds (W.A. Steynberg pers. comm.).

I predict that *Rosa eglanteria* will become increasingly abundant and troublesome throughout the high altitude grasslands situated on the Stormberg and Drakensberg plateaus, i.e. from Molteno northeastwards to the Lesotho border. However any control programmes must take into account its possible value as a food plant and a source of revenue for local people. According to Palmer (1985) there is a factory in the eastern Orange Free State which processes the fruits (hips), making a vitamin syrup. In Lesotho every rose area has its annual rosehip holiday when the children pick the fruits to raise money for their schools.

Populus × *canescens* (Figure 8C), *Salix babylonica* (Figure 8K) and *S. fragilis* (fide R.D. Meikle) (Figure 8L) were the most prominent invaders of watercourses after *Acacia mearnsii*. All three species are large (up to 20 m and more in the case of *P.* × *canescens*), long-lived and can form pure stands along watercourses. *P.* × *canescens*, unlike the other two species, only reproduces by suckering from the roots and in this way can form dense stands. *S. babylonica*, and apparently *S. fragilis*, reproduce only vegetatively in southern Africa from severed branches (Henderson 1991c). Fast-flowing watercourses in the mountainous districts favour the propagation of all three species as well as the dispersal of the *Salix* species. Humans have also assisted the dispersal of *Salix* species by planting truncheons along riverbanks and in riverbeds.

Acacia dealbata (Figure 7B) is potentially the most important invader of watercourses in the Grassland Biome of the eastern Cape. This judgement is based on its invasiveness in the grasslands of the Transvaal (Henderson & Musil 1984), Natal (Henderson 1989), Orange Free State (Henderson 1991a) and Lesotho (Talukdar 1981). Major factors contributing to its success as a riverine invader are its massive production of long-lived seed and the efficient dispersal of seed along watercourses. Dean *et al.* (1986) report a seed longevity of 100 years for *A. dealbata*. Biological control using seed attacking enemies would probably be the most effective method of curtailing the spread of both this species and *A. mearnsii*. Conflicts of interest with the Wattle Industry have halted any research in this direction (H.G. Zimmermann pers. comm.).

Acacia longifolia (Figure 7C) and *Hakea sericea* have invaded mountain fynbos in the eastern Cape. In this survey both species were recorded in the Grahamstown area but only *A. longifolia* was recorded on the mountains near Port Elizabeth. The National Herbarium in Pretoria has a record of *H. sericea* dating back to 1976 on the Van Staden's Mountain. Biological control programmes started in the 1970's (for *H. sericea*) and in the 1980's (for *A. longifolia*) offer a means of reducing their vigour and curtailing their spread. Reductions of up to 80% in annual seed production of both species have been recorded (Dennill 1987; Gordon 1990). An indigenous fungus causing gummosis and death in *H. sericea* is particularly devastating (Morris 1982) and has now been used to produce the world's first mycoherbicide (M.J. Morris pers. comm).

Three *Pinus* species were heavily invasive (i.e. scoring abundance ratings of 5 or more) in parts of the eastern Cape. These were *P. pinaster* (Figure 8B), *P. halepensis* (Figure 8A) and *P. patula*. *P. radiata* was locally abundant. Macdonald & Jarman (1984) ranked *P. pinaster, P. radiata* and *P. halepensis* as the fourth, seventh and eighth most important invaders of the Fynbos Biome. *P. patula* is an important invader of moist montane grasslands in Natal (Macdonald & Jarman 1985) and the Transvaal (Henderson & Musil 1984).

All these pines have winged seeds adapted to wind dispersal. *Pinus radiata* seed is able to travel up to three kilometres from its source (Richardson & Brown 1986). *P. radiata, P. pinaster* and *P. patula* are all reported to regenerate profusely from seed after a fire (Kruger 1977; Richardson & Brown 1986; Wormald 1975). These wind-dispersed and fire-adapted pines are a particular threat to the mountain fynbos and moist subtropical grassland of the eastern Cape.

Rubus affinis (Figure 8J), recorded during this survey, and *R. phoenicolasius* reported by Phillipson (1990) are potentially important invaders in moist subtropical grassland. Both species are well-established near Hogsback in the Amatole Mountains.

Several species which are heavily invasive along the coastline of Natal in Acocks's Coastal Forest and

Thornveld (Henderson 1989), are also invasive in the eastern Cape at the southern limit of the same veld type. These species are *Psidium guajava* (Figure 8F), *Lantana camara* (Figure 7J), *Solanum mauritianum* (Figure 8O) and *Cestrum laevigatum*. They could become serious invaders within this veld type in the eastern Cape which stretches from the Transkei border to about 50 km south of East London near the Keiskamma River.

Chromolaena odorata, not recorded in this survey, is potentially the most important invader of the stretch of coastline just mentioned. It has been rated as the most important invader in Natal (Macdonald & Jarman 1985) and is largely confined to Acocks's Coastal Forest and Thornveld (Henderson 1989).

Pereskia aculeata, a climbing cactus, is another important invader of coastal forest in Natal (Macdonald & Jarman 1985) and a potentially important invader in the eastern Cape. It was not recorded in this survey but has been reported to be spreading in the Grahamstown and Bathurst areas by Jacot Guillarmod (1988).

Leucaena leucocephala, not recorded in this survey, is a potentially valuable fodder and firewood plant, and is also a potential invader of the coastal lowlands of the eastern Cape. This species is invasive in Natal (Macdonald & Jarman 1985) and is a serious weed in several countries in the tropics (Holm *et al*. 1979). The Department of Agricultural Development has up till now prevented the importation of commercial quantities of seed but it does recognise that *Leucaena* has much potential and should be exploited (V.D. Wassermann pers. comm.). Certain cultivars should be promoted in specific areas but this should exclude the Hawaiian type because of its prolific seeding. Consideration is being given to the introduction of suitable seed-eating insects with a view to curbing further spread of this species in affected areas (V.D. Wassermann pers. comm.).

Opuntia stricta commonly known in South Africa as the Australian Pest Pear because it reached pest proportions in Australia (Mann 1970) is another potentially important invader. It was seldom recorded during this survey but it could have been overlooked because of its low stature. It is said to be spreading in the Savanna Biome between Alexandria on the coast and Grahamstown (H.G. Zimmermann pers. comm.) It is also an invader of savanna vegetation in the northern Cape (Henderson 1991), Natal (Henderson 1989), Transvaal (pers. observ.) and Namibia (Brown & Gubb 1986). It has invaded an area of approximately 10 000 ha south of Skukuza in the Kruger National Park situated in the Transvaal (K. Maggs pers. comm.).

Apart from the riverine invaders already mentioned, only a further four species were recorded as heavily invasive (i.e. scoring abundance ratings of 5 or more) in one or more localities. These were *Acacia longifolia* in Howison's Poort near Grahamstown; *Arundo donax* (Figure 7G) on the coast near East London and in *Acacia* savanna near Adelaide; *Ligustrum* sp. in moist subtropical grassland in the Amatole Mountains; and *Sesbania punicea* (Figure 8N) on the coast near East London and along the Gamtoos River valley in the Hankey and Patensie Districts. The latter infestations are being cleared with the use of herbicides (H.G. Zimmermann pers. comm.). There is much confidence that a biological control programme, initiated in the 1980's and using three species of introduced weevils, will halt the invasive spread of this plant in South Africa (Hoffmann & Moran 1988).

Species which have not already been discussed and which were heavily invasive in one or more localities in roadside and veld habitats were: *Eucalyptus diversicolor* on the Elandsberg near Port Elizabeth, and unidentified species of *Eucalyptus* (possibly relics of a dune stabilization programme) in dune vegetation near Port Elizabeth (Figure 7I); *Nicotiana glauca* in karoo vegetation near Jansenville (Figure 7M); *Pennisetum* sp. in coastal vegetation near Kidd's Beach (East London District), and *Ricinus communis* in coastal vegetation near Alexandria and in the Gamtoos River valley near Patensie (Figure 8G).

Ricinus communis has generally been regarded as an introduced species in southern Africa possibly from elsewhere in Africa. However, seeds in excess of 1 200 years old have been discovered in archaeological diggings in the Baviaanskloof near Patensie (Brink 1988). This evidence suggests that, if indeed introduced, primitive hunter-gatherers were the agents (Brink 1988). This is in sharp contrast to the majority of our alien weeds which have been introduced since the colonization of the Cape 300 years ago (Brink 1988; Wells *et al*. 1986).

Fifteen species were locally common in one or more localities. These were *Acacia melanoxylon, Pinus radiata* and *Solanum mauritianum* in the Amatole Mountains near Stutterheim (all three spp.) and Hogsback (*A. melanoxylon*); *Robinia pseudoacacia* (Figure 8H) (watercourses), *Populus* cf. *nigra* (Figure 8D) (watercourses), *Agave americana* (Figure 7F) (watercourses) and *Prunus persica* (Figure 8E) in temperate grassland; *Agave americana* and *Trichocereus* cf. *spachianus* in arid savanna in the Jansenville District; *Atriplex* cf. *nummularia* (Figure 7H) and *Tamarix* cf. *ramosissima* along watercourses in the karroid western parts; *Nerium oleander* (Figure 7L) along the Baviaanskloof River; *Casuarina cunninghamiana* and *Phytolacca dioica* in the Gamtoos River valley in the Hankey and Patensie Districts; *Melia azedarach* (Figure 7K) in disturbed vegetation around East London; *Opuntia vulgaris* in coastal thicket between Port Elizabeth and Alexandria and *Eucalyptus* spp. (Figure 7I) around Grahamstown. Martin & Noel (1960) estimated that between 15 and 20 *Eucalyptus* spp., as well as hybrids, grow in and around Grahamstown. It was not possible to say how many were cultivated only and how many were naturalized.

Agave americana appeared to be spreading from seed in the Kamferspoort and surrounding areas in the Grootrivierberge southwest of Jansenville. Several scattered plants were seen growing in high rocky clefts far from any planted specimens. Large plants with copious seed were seen on the plains below the mountains. This was an unusual sighting since *A. americana* usually spreads only very locally by suckering (pers. obs.). It may also be capable of limited spread from bulbils (small plants produced in the axils of the inflorescence).

Relation of invasion to environmental factors

'From historical data it is clear that vast retrogressive and even radical changes have taken place in the indigenous vegetation of the eastern Cape' (Roux & Van der Vyver 1988). These changes have occurred largely since the settlement of European farmers in this region in about 1770 (Jacot Guillarmod 1988). The deterioration of the indigenous vegetation has been associated with overgrazing, poor management practices, bush-clearing and alien plant invasion (Lubke *et al.* 1986; Roux & Van der Vyver 1988; Teague 1988).

Already by 1776 there were reports that the grazing had started to deteriorate rapidly after only seven or eight years of settlement with cattle in the Camdeboo region near Graaff-Reinet (Jacot Guillarmod 1988). It is in the same region that the prickly pear *Opuntia ficus-indica* was first introduced to the eastern Cape and in which it became a serious problem (MacDonald 1891).

While degradation of the indigenous vegetation opened the way for alien plant invasion, there were other factors which influenced the success of individual species. The successful spread and invasion of large areas by *Opuntia ficus-indica* and *O. aurantiaca* can be largely attributed to their adaptability to the prevailing climatic conditions, their efficient dispersal mechanisms and to the absence of natural predators. MacDonald (1891) reported that the seeds of *O. ficus-indica* were spread in the excreta of humans, baboons, birds, cattle, sheep and goats. Even the Addo elephants, before they were fenced in at the Addo Elephant Park, were reported to eat the fruit of *O. ficus-indica* (Archibald 1955). Today the elephants have virtually eliminated *O. ficus-indica* from the Addo Park (Macdonald 1984). *O. aurantiaca* spreads only vegetatively by detached stem sections. These sections are very spiny and readily attach themselves to animals, clothing, shoes and even vehicles. Stem sections of both *O. ficus-indica* and *O. aurantiaca* are dispersed by water.

The absence of natural predators appears to have been one of the most important factors in the successful invasion of *Opuntia ficus-indica, O. aurantiaca* and *O. vulgaris* in South Africa. This was demonstrated by the dramatic destruction of dense populations of these species, including the almost complete eradication of *O. vulgaris* following the introduction of their natural insect herbivores (Zimmermann *et al.* 1986). Zimmermann *et al.* (1986) conclude that insect herbivores are also likely to play an important role in determining the abundance and distribution of other alien plant species in South Africa.

The success of some invasive species in the eastern Cape has no doubt been aided by their establishment in large plantations. This certainly seems to be the case with species of *Pinus* and *Acacia*. Notable species which have become invasive are *Pinus pinaster, P. halepensis* and *Acacia mearnsii*, all of which have been cultivated commercially for their timber and in the case of *A. mearnsii*, for the tannin in its bark. *P. halepensis, A. cyclops, A. saligna* and *A. pycnantha* were used for driftsand reclamation at Port Elizabeth between 1893 and 1897 (Stirton 1978).

Water, or the lack thereof, has possibly been the most important abiotic factor influencing alien plant invasion in the eastern Cape. In terrestrial habitats, most invasion in terms of species diversity and abundance of invaders was recorded in the wetter eastern parts. With the exception of invasion by a few drought-adapted species, most invasion of the arid central and western interior has been noted only along watercourses.

Watercourses have enabled the long-range dispersal of many species including those which otherwise would be relatively immobile, such as *Acacia mearnsii, A. dealbata, Sesbania punicea* and *Ricinus communis. Salix babylonica* and *S. fragilis* are restricted to watercourses and depend on flowing water for their vegetative dispersal.

Invaders which have successfully invaded fynbos (a fire-adapted vegetation type) have various adaptations which enable them to survive periodic high intensity fires. These adaptations include serotiny (seeds held in heat resistant cones) in *Hakea sericea* and *Pinus pinaster*, and fire-stimulated seed germination in *Acacia longifolia* and *A. mearnsii*.

SOME IDEAS FOR THE FUTURE

Alien plant invasion is likely to increase in all parts of the eastern Cape and particularly in the wetter eastern parts from sea level to an altitude of about 1 300 m. The subregions and their indigenous vegetation types which are most at risk are the coastal belt between the Kei and Keiskamma Rivers (coastal 'forest'), the coastal mountain ranges (mountain fynbos) and southern interior mountain ranges extending from Stutterheim to Somerset East (moist subtropical grassland).

Many invasive species are so well established that their eradication is probably not possible nor feasible. Efforts should however be made to contain their spread and prevent their invasion of new sites. Control programmes should take into account the species complexes which occur in all vegetation categories. The removal of one problem species could simply open the way for other problem species.

Urgent attention should be given to the control, or if possible, the eradication of potentially important invaders which are relatively scarce at this stage. These include *Opuntia stricta* and *Pereskia aculeata*. Steps should be taken to prevent the spread of *Leucaena leucocephala* from plantations. *Chromolaena odorata*, not yet recorded in the eastern Cape, is a potentially serious invader of the coastal belt between the Kei and Keiskamma Rivers. This species must not be allowed to establish itself in the eastern Cape.

Some research priorities suggested are the hydrological impacts of alien plant invaders along watercourses and in mountain catchment areas; the breeding of sterile cultivars of useful but invasive species and methods for the control and utilization of invader species.

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APPENDIX

The names of 130 species of naturalized alien trees, shrubs and climbers are listed. Some non-woody species are included. Names and dates in brackets indicate literature references. (PRE): cited on National Herbarium specimen labels.

Acacia
baileyana F.J. Muell., Bailey's wattle
cyclops A. Cunn. ex G. Don, red eye
dealbata Link, silver wattle
decurrens (J.C. Wendl.) Willd., green wattle
fimbriata A. Cunn. ex G. Don (PRE)

longifolia (Andr.) Willd., long-leaved wattle
mearnsii De Wild., black wattle
melanoxylon R. Br., blackwood
pycnantha Benth. (Stirton 1978), golden wattle
saligna (Labill.) H.L. Wendl., port jackson willow
Agave
americana L., century plant
sisalana Perrine, sisal
Ailanthus altissima (Mill.) Swingle, tree-of-heaven
Alhagi maurorum Medik. (= *A. camelorum* Fisch.) (PRE), camel thorn bush
Anredera baselloides (H.B.K.) Baill. (Martin & Noel 1960)
Araujia sericifera Brot. (Martin & Noel 1960), moth catcher
Arundo donax L., giant reed
Atriplex cf. *nummularia* Lindl., old man saltbush
Bambusa cf. *balcooa* Roxb. ex Roxb., common bamboo
Bambuseae sp. (small unidentified bamboo)
Caesalpinia
decapetala (Roth) Alston, Mauritius thorn
gilliesii (Wallich. ex Hook.) Benth., bird-of-paradise
Callistemon citrinus (Curtis) Stapf (PRE), lemon bottlebrush
Canna indica L. (Martin & Noel 1960), canna
Cardiospermum grandiflorum Schwartz (PRE), balloon vine
Casuarina cunninghamiana Miq., beefwood
Cereus peruvianus (L.) Mill. [= cf. *jamacaru* DC. (fide H.F. Glen, pers. comm.)], queen of the night
Cestrum laevigatum Schlechtd., inkberry
Citrus sp. (Martin & Noel 1960)
Cortaderia sp., pampas grass
Cotoneaster sp., cotoneaster
Crataegus monogyna Jacq. (PRE), English hawthorn
Crotalaria sp.
Cupressus arizonica Greene, Arizona cypress
Cydonia oblonga Mill., quince
Cyphomandra betacea (Cav.) Sendtn. (Stirton 1979), tree tomato
Cytisus scoparius L. (PRE), Scotch broom
Eucalyptus
cladocalyx F.J. Muell., sugar gum
diversicolor F.J. Muell., karri gum
ficifolia F.J. Muell., red flowering gum
globulus Labill. (Salisbury 1919)
grandis Hill. ex Maid. (= *E. saligna* Sm.) (Stirton 1979), saligna gum
lehmannii (Schauer) Benth., spider gum
sp. cf. *camaldulensis* Dehnh., red gum
Ficus
carica L., edible fig
?sp., fig
Fraxinus cf. *americana* L., American ash
Gleditsia triacanthos L., honey locust
Glycyrrhiza glabra L. (PRE), liquorice
Grevillea robusta A. Cunn. (L. Henderson, pers. observ. 1981), Australian silky oak
Hakea sericea Schrad., silky hakea
?*Hylocereus* sp.
Ipomoea
alba L. (PRE), moon flower
congesta R. Br. (Martin & Noel 1960)
purpurea (L.) Roth (Phillipson 1987), common morning glory
Jacaranda mimosifolia D. Don, jacaranda
?*Juniperus* sp., juniper
?*Lagerstroemia indica* L., pride-of-India
Lantana camara L., lantana
Lavatera arborea L. (Salisbury 1919), tree mallow
Leptospermum laevigatum (Soland. ex Gaertn.) F.J. Muell., Australian myrtle
Ligustrum
japonicum Thunb. (PRE), Japanese privet
sinense Lour., privet
?sp., privet
Melia azedarach L., syringa
Morus alba L., white mulberry
Myoporum tenuifolium Forst. f. subsp. *montanum* (R. Br.) Chinnock (PRE), manatoka tree
Nerium oleander L., oleander
Nicotiana glauca R.C. Grah., wild tobacco
Opuntia
aurantiaca Lindl. (Stirton 1978), jointed cactus
ficus-indica (L.) Mill., sweet prickly pear
imbricata (Haw.) DC., chain-link cactus
lindheimeri Engelm., small round-leaved prickly pear
stricta Haw., pest pear of Australia
vulgaris Mill., cochineal prickly pear
sp. cf. *robusta* cultivars, spineless prickly pears
Paraserianthes lophantha (Willd.) Nielsen subsp. *lophantha*, stinkbean
Parkinsonia aculeata L., Jerusalem thorn
Passiflora caerulea L., blue passionflower
Pennisetum sp.
Pereskia aculeata Mill. (Martin & Noel 1960), Barbados gooseberry
Phoenix cf. *dactylifera* L., real date palm
Phytolacca dioica L., belhambra
Pinus
?*elliottii* Engelm., slash pine
halepensis Mill., aleppo pine
patula Schlechtd. & Cham., patula pine
pinaster Ait., cluster pine
pinea L., umbrella pine
radiata D. Don., radiata pine
roxburghii Sarg., chir pine
Populus
× *canescens* (Ait.) J.E. Sm., grey poplar
sp. cf. *deltoides* Bartr. ex Marsh., match poplar
sp. cf. *nigra* var. *italica* Muenchh., Lombardy poplar
Prosopis spp. (*P. glandulosa* Torr. var. *torreyana*, mesquite; and possibly other taxa)
Prunus
armeniaca L., common apricot
persica (L.) Batsch, peach
sp. cf. *japonica* Thunb. (PRE), Japanese bush cherry
Psidium guajava L., guava
Pyracantha
angustifolia (Franch.) C.K. Schneid., yellow firethorn
?*crenulata* (D. Don) M.J. Roem., firethorn
Quercus robur L. (Phillipson 1987), English oak
Ricinus communis L., castor-oil plant
Robinia pseudoacacia L., black locust
Rosa
eglanteria L., eglantine
odorata (Andr.) Sweet (Phillipson 1987), tea rose
Rubus
affinis Weihe & Nees, blackberry
phoenicolasius Maxim. (Phillipson 1990), wineberry
Salix
babylonica L., weeping willow
caprea L., pussy willow
fragilis L. (fide R.D. Meikle pers. comm.), basket willow
Sambucus sp., elder
Schinus molle L., pepper tree
Senna
corymbosa (Lam.) Irwin & Barneby (Gordon-Gray 1977), autumn 'cassia'
didymobotrya (Fresen.) Irwin & Barneby, peanut-butter 'cassia'
multiglandulosa (Jacq.) Irwin & Barneby (Gordon-Gray 1977)
occidentalis (L.) Link (Schonland 1919), wild coffee
septemtrionalis (Viv.) Irwin & Barneby, arsenic bush
Sesbania
punicea (Cav.) Benth., red sesbania
virgata (Cav.) Persoon. (Jacot Guillarmod 1988)
Solanum
hispidum Pers., devil's fig
mauritianum Scop., bug tree
pseudocapsicum L. (Phillipson 1987), Jerusalem cherry
sarrachoides Sendtner (Phillipson 1990)
seaforthianum Andr., potato creeper
Tamarix cf. *ramosissima* Ledeb., pink tamarisk
Trichocereus cf. *spachianus* (Lemaire) Riccobono, torch cactus
Ulex europaeus L. (Phillipson 1987), gorse
Ulmus spp., elms; at least two spp.
?*Washingtonia* sp., petticoat palm
Yucca aloifolia L. (Martin & Noel 1960), Spanish bayonet

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The Ven. Charles Theophilus Hahn, a hitherto unknown Edwardian botanical illustrator in Natal, 1908–1916

J.P. ROURKE* and J.C. MANNING*

Keywords: botanical art, C.T. Hahn, early 20th century, Natal flora

ABSTRACT

A brief biographical sketch is given of the Rev. C.T. Hahn, an English-born, Oxford-educated Anglican missionary in Zululand who painted some 235 watercolours of Natal flora between 1908 and 1913. Hahn (who later changed his name to Headley) was one of the most productive of the early botanical illustrators in Natal but as a collection of his paintings has only recently been discovered, his work has until hitherto remained unknown.

UITTREKSEL

'n Kort lewensskets van eerw. C.T. Hahn word gegee. Hy is in Engeland gebore, het aan Oxford studeer en is later as Anglikaanse sendeling na Zoeloeland. Van 1908 tot 1913 het hy die Natalse flora in sowat 235 waterverfskilderye afgebeeld. Hahn (wat sy naam later na Headley verander het) was een van die produktiefste vroeë botaniese illustreerders in Natal. Omdat 'n versameling van sy skilderye eers onlangs ontdek is, was sy werk tot dusver onbekend.

INTRODUCTION

In February 1988 a collection of 235 original water colour illustrations of Natal flora dating from 1908 to 1916 was brought to the Compton Herbarium, Kirstenbosch for identification and cataloging. These paintings are the work of the Rev. C.T. Hahn, an Anglican missionary who in 1909 became priest in charge of Empangeni and Inhlwati in the Diocese of Zululand. The artist is not listed in Desmond (1977), Gordon-Brown (1975), Gunn & Codd (1981), or Lanjouw & Stafleu (1954 et seq.) either as a botanical illustrator or plant collector. Indeed, nothing appears to have been recorded about Hahn's activities as an artist—particularly in respect of his botanical paintings, and as there is the ever present possibility that the collection may be fragmented and dispersed, a list of these works is published here as a permanent record together with the few biographical details currently available to us.

Hahn appears to have been a shy, self-effacing personality whose work has only recently come to light. His botanical paintings are accurate and have considerable charm apart from their inherent historical interest. Executed under primitive field conditions, they were evidently not undertaken with a scientific motif in mind but rather for his personal satisfaction and relaxation, or perhaps, merely as a record of his period of temporary residence in South Africa.

BRIEF BIOGRAPHY

Charles Theophilus Hahn, the only son of Theophilus Sigmund Hahn and Helen Marfield Hahn (formerly Walters) was born on 1st March 1870 at Wandsworth, Surrey, south London but was subsequently brought up in the village of Headley in Hampshire. As a young man, he entered Pembroke College, Oxford, graduating a B.A. in 1892 and later an M.A. in 1895. Shortly after receiving his first degree he decided to take up the ministry and in 1892 embarked upon a period of training at the Leeds Clergy School. He was ordained a deacon in 1893 and a priest in 1894. Hahn held various church appointments in England before coming to South Africa to undertake missionary work. We have not been able to establish precisely when he arrived in South Africa. Nevertheless, a landscape painting titled 'On the road to Pretoria' dated May 1906 establishes the earliest date of his residence here that we have traced so far.

His first posting in South Africa was as curate of Etalaneni in 1908. In 1909 he became priest-in-charge of Empangeni and Inhlwati ('Nhlwati) in the Diocese of Zululand—a position in which he remained until 1913 when he became Archdeacon of Eshowe and Canon of St Peters, Vryheid. It was during this period (1908–1913) that the great majority of his botanical paintings were executed (about 200 out of 286). While at Vryheid, however, he continued to paint, often visiting his old haunts at Empangeni, Nongoma and the Mission at Inhlwati. Hahn's output was surprisingly high. In one month for example (November 1911) he completed 11 paintings, that is approximately one every three days. Indeed, one wonders how much missionary work he undertook during this phase of his life which seems to have been very largely devoted to painting flowers.

In 1917 Hahn returned to England to become Vicar of Pontefact but shortly afterwards joined the Church Army serving in France, 1918, 1919 (Figure 1). It was at about this time that he changed his name from Hahn to Headley, using the name of his former home village in Hampshire as his new surname. This rather drastic step was presumably taken in response to anti-German sentiments prevailing at that time in Britain. Throughout this article we have used the name Hahn rather than Headley as the botanical illustrations executed in Natal were completed before he changed his name.

* National Botanical Institute, Kirstenbosch, Private Bag X7, Claremont 7735.

MS. received: 1991-05-15.

FIGURE 1.—Charles Theophilus Hahn, in a Church Army uniform, ± 1919.

By 1919 he was back in South Africa where as C.T. Headley he served as Sub Dean of St George's Cathedral, Cape Town, until 1922, later moving to South West Africa (now Namibia) as priest-in-charge at Keetmanshoop from 1922 till 1924 and Archdeacon of Damaraland from 1924 until 1927. When he returned to Britain he took up a position in the Diocese of Chelmsford, Essex. Charles Theophilus Headley died at Holborn, London on 16th September 1930 aged 60.

DESCRIPTION OF THE BOTANICAL COLLECTION

The artwork is on sheets of creamy-white (possibly hand made) paper of variable size, cut to suit the subjects, all of which are depicted life size. Each plate is labelled with a date (month and year) and a sequence number in either the lower left or lower right hand corner. They are mounted centrally on light-weight brown manilla sheets measuring 460 × 355 mm, reinforced along the left hand margin with a strip of manilla perforated in four places to facilitate loose binding. Traces of a gold silk cord were found threaded through the perforations suggesting that a cord binding was originally used to hold the collection together.

In the lower right hand corner of each manilla mounting sheet, locality data is inscribed in ink in long hand. All the botanical plates we examined were unsigned. At the top left hand corner of the manilla mounting sheet the family name appears in printed script in Hahn's hand preceded by its Bentham & Hooker sequence number. In many instances an identification to genus and species is also provided. These determinations as well as the occasional English or African vernacular name are in the same printed script, presumably Hahn's.

Great pains were evidently taken to have his subjects correctly identified. Where this has been done to species level the determinations are invariably correct or bear names that are now merely nomenclaturally outdated. It thus seems highly probable that he was assisted by a competent botanist, possibly J. Medley Wood (Figure 2).

Other paintings by the artist

Hahn was also an accomplished landscape artist whose work depicts scenery in various parts of the world including South Africa. We were informed by two of the owners of the Hahn collection, Mr D. Cope and Mr J. Wessels, that a portion of the collection purchased by them in London during 1984, contained topographical watercolours of east Africa (mainly harbour scenes) and also sketches done in South America, India, Spain, Italy and South West Africa (now Namibia). In 1986 the collection was augmented by the purchase of 235 plates of Natal flora from Hahn's heirs which are the subject of this paper. A Transvaal landscape and an interior scene in a mission church in Natal, both completed during his South African sojourn, are reproduced here as examples of his non-botanical work (Figure 3).

Comments on Hahn's botanical paintings

Hahn has a free and bold style. The plant outline was no more than roughly pencilled to establish placement and proportions before colouring. The paint is applied in bold, somewhat wet strokes, rather than graded washes or with a dry brush technique as practised by Arabella Roupell, Emily Thwaits and Ethel May Dixie. The relative speed of the technique which he employed would have enabled Hahn to achieve the prodigious amount of work which he did. The colours are very faithful, and still vibrant, and the quality of the paintings remarkably consistent: those done in 1910 are barely to be distinguished from those of five years later. The first few paintings, done in Durban in 1909 (*Argemone, Tecomaria* and *Scaevola*), although of comparable style to the remainder, are smaller, and depict a rather modest and meagre part of the plant, unlike the confident and generous representations executed later. The facies of the plant are highly natural and the modelling and texturing good. He succeeded in capturing the lustre on glossy leaves without resorting to oils or transparent glazes as did Katharine Saunders. The style and composition is much more modern than that of Sanderson and Saunders, and the arrangement of the plant parts on the page spatially informed and aesthetically pleasing, and not at all contrived. In some of Saunders' paintings, for example, the plant is abruptly bent beneath the flower to display a top view of the flower but side view of the plant; or the leaves may be splayed out and flattened unnaturally; or the flowers artfully arranged in isolation amongst the foliage; and in some the flowers are even morphologically upside down. Saunders' illustrations, however, stand apart

FIGURE 2.—Examples of C.T. Hahn's botanical illustrations: A, *Erythrina latissima* E. Mey.; B, *Ricinus communis* L.; C, *Ochna serrulata* (Hochst.) Walp.; D, *Hibiscus calyphyllus* Cav. The captions at the base of each illustration are in Hahn's hand.

A

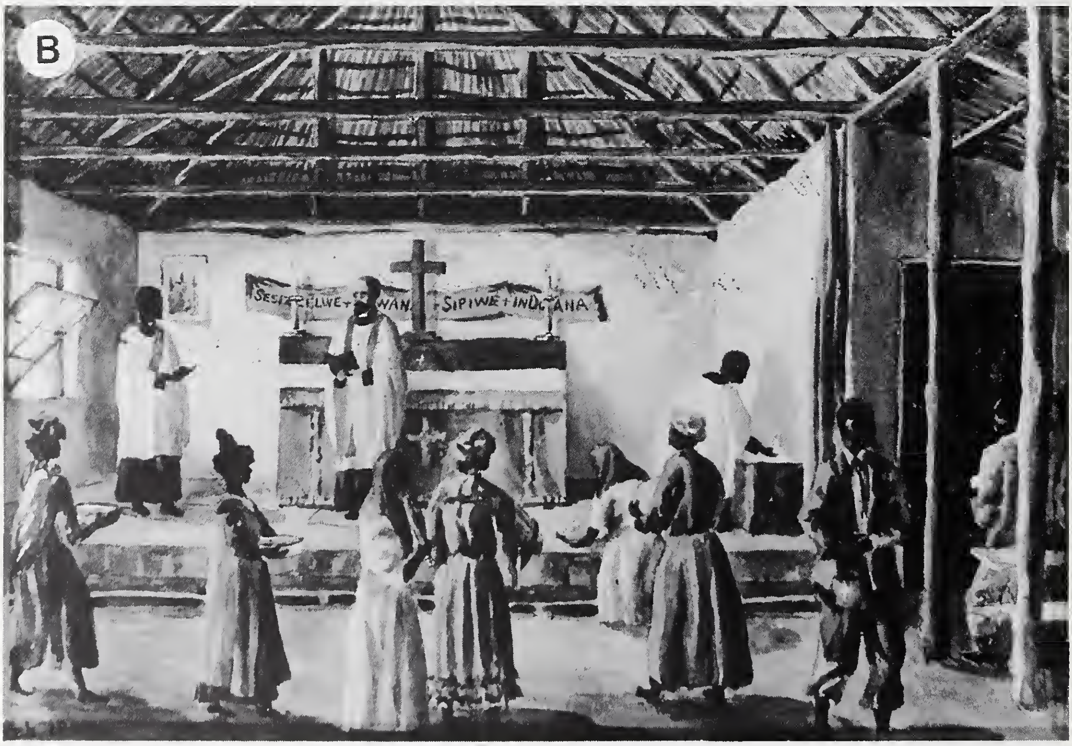

FIGURE 3.—A, an example of a landscape in watercolours, titled 'On the road to Pretoria' (with a waterfall in the Watersmeet Valley, Lyton in the foreground, May 29–31, 1906) signed C.T.H. B, an unusual view by C.T. Hahn of the interior of a mission church in watercolours, titled 'i Babanango Out-Station. The Offertory at Holy Communion. Feb. 1909'. Unsigned.

in the floral dissections which accompany some, indicating an intimate knowledge of plant structure, presumably reflecting the botanically scientific influence of McKen or Wood.

Hahn's illustrations present rather complete representations of the species, much as in good herbarium specimens, displaying aspects of the branching pattern, phyllotaxy, inflorescence morphology, etc. which aids identification greatly, unlike the frequently piecemeal fragments illustrated by Saunders. Also, each species has a plate alone, although different stages of the same may be included: the decorative floral bouquets of Victorian artists are eschewed in favour of a more austere approach. Hahn's scientific and botanically educated mind is evident in the careful combination of fruiting and flowering stems of a number of species, necessitating re-collecting of material later in the season, and in the inclusion of the underground parts of most of the monocotyledons, which are important characters in this group. It is clear that Hahn systematically set about recording the flora, both indigenous and naturalised (but not exotic) of his immediate vicinity, and avoided those species not native to the area. The inclusion of the native names of many is an interesting point. His intention in painting the plants was clearly different from that of Saunders, whose primary interest was in the beauty of the flowers.

EARLY BOTANICAL EXPLORATION OF NATAL

Natal was first explored botanically by J.F. Drège who, in 1832, travelled along the coast from Grahamstown to Durban as a member of Dr Andrew Smith's expedition to Zululand. He was followed by two other pioneers, Drs W. Gueinzius in 1838 and F. Krauss in 1842, both of whom collected in and around Durban, the latter with an occasional foray into the Natal interior. With the declaration of British sovereignty over Natal in 1843, the German phase came to an end, but a stream of settler botanists began to enter the colony from Britain. These, with the dates of their arrival, were Dr W. Stanger (1844), the Fannin family (1847), M.J. McKen and J. Sanderson (1850), R.W. Plant and J.M. Wood (1852), the Saunders family (1854) and W.T. Gerrard (1856). Of these, all except Stanger (Colonial Geologist) and the Fannins (who settled in the Midlands) purchased farms in the Tongaat area just north of Durban. It seems that the Saunders' homestead in particular became a convenient rendezvous for North Coast botanists (Bayer 1979). McKen, Sanderson, Plant, Wood and Gerrard were by far the most active Natal plant collectors of the last century. The Rev. J. Buchanan, who arrived in Natal in 1861 was at one time in charge of the Presbyterian Mission at Mapumulo, north of Tongaat, and collected also with McKen, but left the Colony in 1874.

Hahn arrived in Natal in 1908, some 50 years after this concentrated influx of settler botanists. His work as an illustrator of Natal plants was preceded by that of Sanderson and Saunders. Both these artists were well acquainted with other collectors in Natal and with the botanists at Kew, forming, as it were, a social-scientific circle north of Durban where their farms lay, which was the hub of botanical interest in the colony. It was to the Saunders' home that Marianne North, the celebrated botanical and landscape artist, came in 1883 when she visited Natal. Hahn arrived in Natal too late to join this network. Katharine Saunders died in 1901. Gerrard had left Natal for Madagascar in 1864; Plant had died in 1858; and McKen in 1871. Medley Wood, succeeding as Curator of the Durban Botanical Gardens in 1882, although available, was no longer young when Hahn was working, and died suddenly at his desk in 1915, aged 88. His death corresponds almost exactly with the cessation of Hahn's work in 1916. We have been unable to establish whether Medley Wood and Hahn ever met although it seems highly probable that they were acquainted.

ACKNOWLEDGEMENTS

The authors are indebted to Mr D. Cope, Mr J. Wessels and Mrs Nancy Claire Foster, owners of the Hahn Collection for bringing these paintings to our attention, for granting permission to reproduce selected items in this article, and for certain biographical information. We are also most grateful to the Librarians of Pembroke College, Oxford and Lambeth Palace, London for further biographical data. The precise details regarding Hahn's birth and death were obtained by personal search (JPR) at the Office of Population Censuses and Surveys, St Catherine's House, London.

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APPENDIX

LIST OF BOTANICAL PLATES EXAMINED BY THE AUTHORS

In this list the 235 plates are arranged by plant families. The numbers after the species name are Hahn's numbers which appear on the lower right (occasionally lower left) hand corner of each illustration. A set of xerox photocopies of all the illustrations listed here is filed in the archives of the Compton Herbarium.

MONOCOTYLEDONS

ARACEAE

Zantedeschia aethiopica (L.) Spreng., 124, Nov. 1911, found in marshy ground at 'Nhlwati.

Zantedeschia jucunda Letty, 234, Nov. 1913, grown in a garden at Nongoma from a bulb sent from Swaziland.

Zantedeschia rehmannii Engl., 29, Nov. 1910, found in the grass among scrubby bush near Mhlopekulu, Nongoma.

COMMELINACEAE

Aneilema aequinoctiale (P. Beauv.) Loudon, 156, April 1912, found in the bush at Amatshemhlope.

Commelina africana L., 18, Sept. 1910, found as a weed in the garden at Nongoma.

Commelina diffusa Burm. f. subsp. *diffusa*, 24, Nov. 1910, found in an old mealie garden at 'Nhlwati.

Cyanotis speciosa (L. f.) Hassk., 69, Mar. & Dec. 1911, found in the veld at Nongoma.

Murdannia simplex (Vahl) Brenan, 275, Jan. 1916, found near a stream at Empangeni.

LILIACEAE

Agapanthus praecox Willd., 56, Jan. 1911, found in the veld at Nongoma.

Albuca angolensis Welw., 238, Jan. 1914, found in the veld near the Emadundwini on the Nongoma-Hlabisa road.

Albuca nelsonii N.E. Br., 78, May 1911, found in the veld at Nongoma.

Aloe arborescens Mill., 163, May 1912, found beneath a high rocky krantz in veld at Vryheid.

Aloe arborescens Mill., 208, June 1913, found in a donga among big rocks at Nongoma.

Aloe boylii Bak., 27, Nov. 1910, found in the veld at 'Nhlwati.

Aloe ecklonis Salm-Dyck, 7, Aug. 1910, found in the veld at Nongoma.

Aloe kraussii Bak., 134, Jan. 1912, found in the open veld at 'Nhlwati.

Aloe parviflora Bak., 155, March 1912, found in the veld at 'Nhlwati.

Aloe saponaria (Ait.) Haw., 175, July 1912, found in the bushveld near the Wela, on 'Nhlwati rd.

Aloe spectabilis Reynolds, 164, May 1912, found in the bare stony veld on the top of Ngome.

Androcymbium natalense Bak., 88, July 1911, found in the veld at 'Nhlwati.

Anthericum cooperi Bak., 197, Oct. 1912, found in the veld at 'Nhlwati.

Bulbine asphodeloides (L.) Roem. & Schult., 84, June 1911, found in the veld at Mhlopekulu, near Nongoma.

Dipcadi cf. *viride* (L.) Moench, 167, May 1912, found in the veld at Nongoma.

Dipcadi viride (L.) Moench, 23, Oct. 1910, found in the veld at Nongoma.

Gloriosa superba L., 278, Jan. 1916, found in the bush on the sand dunes on the foreshore at Durban.

Kniphofia gracilis Harv. & Bak., 147, Feb. 1912, found in the veld at Nongoma.

Kniphofia triangularis Kunth, 83, June 1911, found in the veld at Hlabisa.

Kniphofia tysonii Bak., 65, March 1911, found in the veld at Nongoma.

Ledebouria revoluta (L. f.) Jessop, 2, Aug. 1910, found in the veld at Nongoma.

Protasparagus densiflorus (Kunth) Oberm., 194, Sept. 1912, found in the bushveld near the Wela stream on the way to 'Nhlwati.

Protasparagus racemosus (Wild.) Oberm., 201, Dec. 1912, found in the veld at Nongoma.

Sandersonia aurantiaca Hook., 30, Nov. 1910, found among grass in scrubby bush at Nongoma.

Scilla nervosa (Burch.) Jessop, 127, Nov. 1911, found in the veld at 'Nhlwati.

Tulbaghia ludwigiana Harv., 20, Oct. 1910, found in the veld at Nongoma.

Urginea macrocentra Bak., 192, Sept. 1912, found in the veld at 'Nhlwati.

AMARYLLIDACEAE

Apodolirion buchananii Bak., 90, July 1911, found in the veld at 'Nhlwati.

Boophane disticha (L. f.) Herb., 13, Sept. 1910, found in the veld near Mona stream, Nongoma.

Brunsvigia radulosa Herb., 53, Jan. 1911, found in the veld at Nongoma.

Crinum macowanii Bak., 229, Oct. 1913, found by the Mkiwaneni near 'Nhlwati.

Cyrtanthus brachyscyphus Bak., 199, Oct. 1912, found on the banks of a stream on the Nongoma-Ngome track, near Ngongomane Hill.

Cyrtanthus breviflorus Harv., 1, Aug. 1910, found on swampy ground by a stream at Eshowe.

Cyrtanthus contractus N.E. Br., 190, Aug. 1912, found in the veld in the thorns near the Wela on 'Nhlwati track.

Cyrtanthus tuckii Bak., 15, Sept. 1910, found in the veld at Nongoma.

Nerine appendiculata Bak., 81, May 1911, found by the side of a stream in Ngome forest.

Scadoxus puniceus (L.) Fries & Nordal, 93, Aug. 1911, found in the veld at 'Nhlwati.

HYPOXIDACEAE

Hypoxis angustifolia Lam., 6, Aug. 1910, found in veld by Mona stream on Nongoma road.

Hypoxis filiformis Bak., 216, Aug. 1913, found in a damp donga at Nongoma.

Hypoxis gerrardii Bak., 79, May 1911, found in the veld at Nongoma.

Hypoxis rooperi Moore, 16, Sept. 1910, found in the veld at Nongoma.

DIOSCOREACEAE

Dioscorea diversifolia Griseb., 138, Jan. 1912, found among thick tangle of shrubs and tall grass on banks of stream at 'Nhlwati.

IRIDACEAE

Anomatheca laxa (Thunb.) Goldbl., 110, Oct. 1911, found in the bush, near the waterfall at 'Nhlwati.

Aristea cognata Weimarck, 26, Nov. 1910, found in the veld at 'Nhlwati'.

Aristea ecklonii Bak., 143, Jan. 1912, found in the open veld at 'Nhlwati.

Dierama pendulum Bak., 92, Aug. 1911, found in the veld at 'Nhlwati.

Dietes butcheriana Gerstner, 152, Feb. 1912, found on the banks of the Umkunzana stream near Tokazi.

Dietes iridoides (L.) Klatt, 203, May 1913, found in the bush, by the waterfall at 'Nhlwati.

Gladiolus dalenii Van Geel, 50, Jan. 1911, found in the veld at Nongoma.

Gladiolus ecklonii Lehm. subsp. *ecklonii*, 46, Dec. 1910, found in the veld at 'Nhlwati.

Gladiolus longicollis Bak. var. *platypetalus* (Bak.) Oberm., 19, Oct. 1910, found in the veld at 'Nhlwati.

Gladiolus papilio Hook.f., 45, Dec. 1910, found in the veld at 'Nhlwati.

Moraea elliotii Bak., 43, Dec. 1910, found in the veld at Isandhlwana.

Moraea spathulata (L. f.) Klatt, 98, Sept. 1911, found in the veld at Ngome.

Moraea stricta Bak., 89, Dec. 1910, found in the veld at 'Nhlwati.

Schizostylis coccinea Backh. & Harv., 149, Feb. 1912, found on the banks of a stream near Ngongomane Hill.

Tritonia lineata (Salisb.) Ker-Gawl. var. *lineata*, 95, Aug. 1911, found in the veld at 'Nhlwati.

Watsonia sp., 60, Feb. 1911, found in the veld at Nongoma.

STRELITZIACEAE

Strelitzia reginae Banks ex Ait., (no number), Aug. 1916, found in damp situations near the Kulu stream, Mtondweni, Empangeni.

ORCHIDACEAE

Bonatea speciosa (L. f.) Willd., 131, Dec. 1911, found in veld among tufts of grass at Alfa (on Ngome-Vryheid road).

Calanthe sylvatica (Thou.) Lindl., 280, Feb. 1916, found in the veld at Ngome.

Disperis stenoplectron Reichb. f., 250, March 1914, found in the veld at Ngome.

Eulophia clavicornis Lindl. var. *clavicornis*, 189, Aug. 1912, found in the veld at Nongoma.

Eulophia clavicornis Lindl. var. *inaequalis* (Schltr.) A.V. Hall, 10, Sept. 1910, found in the veld at Nongoma.

Eulophia clavicornis Lindl. var. *nutans* (Sond.) A.V. Hall, 144, Jan. 1912, found in open veld at Ngome.

Eulophia clitellifera (Reichb. f.) H. Bol., 8, Sept. 1910, found in the veld at Nongoma.

Eulophia ensata Lindl., 239, Jan. 1914, found in the veld at Nongoma.

Eulophia foliosa (Lindl.) H. Bol., 200, Dec. 1912, found in the veld at Nongoma.

Eulophia leontoglossa Reichb. f., 33, Nov. 1910, found in the veld at Nongoma.

Eulophia odontoglossa Reichb. f., 47, Dec. 1910, found in the veld at Nongoma.

Eulophia parviflora (Lindl.) A.V. Hall, 259, Sept. 1915, found in the veld at Empangeni.

Eulophia streptopetala Lindl., 128, Nov. 1911, found in the long grass by the Wela stream, between Empangeni and 'Nhlwati.

Eulophia zeyheriana Sond., 122, Nov. 1911, found in the veld where ground somewhat swampy at 'Nhlwati.

Habenaria clavata (Lindl.) Reichb. f., 52, Jan. 1911, found in the veld at 'Nhlwati.

Habenaria falcicornis (Lindl.) H. Bol. subsp. *caffra* (Schltr.) J.C. Manning, 279, Jan. 1916, found in the veld at Nongoma.

Satyrium parviflorum Sw., 187, Aug. 1912, found in the veld at Ngome.

Schizochilus gerrardii (Reichb. f.) H. Bol., 130, Dec. 1911, found in the veld at Ngome.

DICOTYLEDONS

PROTEACEAE

Protea gaguedi Gmel., 245, Feb. 1914, found on the slopes of Mahashini Hill.

BALANOPHORACEAE
Sarcophyte sanguinea Sparrm., 222, Sept. 1913, found beneath the fever trees near the Umkuze drift at the foot of Ubombo Mtn.

POLYGONACEAE
Achyranthes aspera L., 206, May 1913, found by the roadside at Nongoma.
Cyathula uncinulata (Schrad.) Schinz, 165, May 1912, found among bushes by the roadside at Nongoma.
Polygonum pulchrum Blume, 170, June 1912, found in swampy ground by side of a stream at 'Nhlwati.

AIZOACEAE
Aptenia cordifolia (L. f.) N.E. Br., 116, Oct. 1911, found among some scrubby bushes at Nongoma.
Carpobrotus dimidiatus (Haw.) L. Bol., 211, June 1913, found on the sand dunes on Durban foreshore.
Delosperma galpinii L. Bol., 28, Nov. 1910, found in the veld at Empugwini.

CARYOPHYLLACEAE
Dianthus zeyheri Sond., 273, Dec. 1913, found in the veld at Vryheid.

NYMPHAEACEAE
Nymphaea capensis Thunb., 132, Jan. 1912, found in a vlei at 'Nhlwati.

RANUNCULACEAE
Ranunculus multifidus Forssk., 117, Oct. 1911, found by the side of a stream near the Ngonomane Hill, Ngome.

PAPAVERACEAE
Argemone mexicana L., 105, Oct. 29, 1908, found by the Umgeni River at Umgeni, near Durban.

CAPPARACEAE
Maerua caffra (DC.) Pax, 17, Sept. 1910, found in the open veld at Nongoma.

CRASSULACEAE
Cotyledon orbiculata L., 253, July 1915, found among the rocks on the top of Dupumbane Mtn.
Crassula alba Forssk. var. *parvisepala* (Schoenl.) Toelken, 68, Mar. 1911, found on rocky ground at Ngome.
Crassula pellucida L., 173, June 1912, found on swampy ground at 'Nhlwati.
Crassula vaginata Eckl. & Zeyh., 284, Apr. 1916, found in the veld at 'Nhlwati.
Kalanchoe rotundifolia Haw., 182, Aug. 1912, found among the rocks on the top of 'Nhlwati.

ROSACEAE
Agrimonia odorata Mill., 158, April 1912, found as a weed in the garden at Nongoma.

FABACEAE
Acacia karroo Hayne, 240, Jan. 1914, found in the veld at Nongoma (Framed).
Acacia xanthophloea Benth., 226, Sept. 1913, found in the valley below Imbala ridge on Ubombo road.
Argyrolobium aff. *tomentosum* (Andr.) Druce, 137, Jan. 1912, found in the open veld at 'Nhlwati.
Argyrolobium sp., 272, Nov. 1915, found among rocks on the edge of a krantz at Nongoma.
Cassia floribunda Cav., 146, Feb. 1912, found at the edge of bush at Ngome.
Crotalaria capensis Jacq., 63, Feb. 1911, found in the veld at Nongoma.
Eriosema cordatum E. Mey., 221, Aug. 1913, found in the veld at Nongoma.
Eriosema salignum E. Mey., 143, Jan. 1912, found in the open veld at 'Nhlwati.
Erythrina humeana Spreng., 61, Feb. 1911, found in the veld at Nongoma.
Erythrina latissima E. Mey., 191, (flower Sept. 1912; pod July 1912), found on the slopes of the Mthwadhlane.
Erythrina lysistemon Hutch., 94, Aug. 1911, found in the bush at 'Nhlwati.
Lotononis corymbosa Benth., 102, Sept. 1911, found in the open veld at Nongoma.
Schotia brachypetala Sond., 265, Oct. 1915, found in the thornbush near the Wela on the way to 'Nhlwati.
Sphenostylis angustifolia Sond., 266, Oct. 1915, found in the veld at the edge of the bush at 'Nhlwati.
Tephrosia elongata E. Mey., 153, March 1912, found in the veld at 'Nhlwati (Framed).
Tephrosia macropoda (E. Mey.) Harv., 59, Feb. 1911, found in the open veld at Nongoma.
Vigna luteola (Jacq.) Benth., 125, Nov. 1911, found among the tangled growth on marshy ground at 'Nhlwati.
Vigna unguiculata (L.) Walp., 11, Sept. 1910, found in the open veld at Nongoma.

GERANIACEAE
Geranium flanaganii Knuth, 268, Oct. 1915, found among the bushes by a stream at 'Nhlwati.
Monsonia grandifolia Knuth, 198, Oct. 1912, found in the veld at 'Nhlwati.
Pelargonium luridum (Andr.) Sweet, 111, Oct. 1911, found in the veld at 'Nhlwati.

OXALIDACEAE
Oxalis corniculata L., 166, May 1912, found as a weed in the garden at Nongoma.
Oxalis obliquifolia Steud. ex A. Rich., 34, Nov. 1910, found in the veld at Nongoma.
Oxalis semiloba Sond., 91, July 1911, found in the veld at 'Nhlwati.

RUTACEAE
Calodendrum capense (L. f.) Thunb., 119, Nov. 1911, found in the bush at 'Nhlwati, Zululand.

MALPIGHIACEAE
Acridocarpus natalitius A. Juss., 112, Oct. 1911, found in the bush at 'Nhlwati.

POLYGALACEAE
Polygala virgata Thunb., 207, May 1913, found in the Induna bush, Nongoma.

EUPHORBIACEAE
Clutia sp., 181, Aug. 1912, found in the veld at 'Nhlwati.
Dalechampia capensis Spreng., 141, Jan. 1912, found in the bush at 'Nhlwati.
Euphorbia grandicornis Goebel ex N.E. Br., 205, May 1913, found among the thorn bush near the Black Umfolozi drift.
Euphorbia ingens E. Mey. ex Boiss., 73, Apr. 1911, found in the thorn country below 'Nhlwati, near the Wela.
Euphorbia striata Thunb., 188, Aug. 1912, found by the roadside at Ngome.
Euphorbia trichadenia Pax, 233, Nov. 1913, found in the veld in the thorns near Wela on the way to 'Nhlwati.
Jatropha hirsuta Hochst., 270, Oct. 1915, found in the veld in the thorns by the Wela on the way to 'Nhlwati.
Jatropha sp., 181, Aug. 1912, found in the veld at 'Nhlwati.
Ricinus communis L., 177, July 1912, found in an old garden at 'Nhlwati.

MALVACEAE
Abutilon sonneratianum (Cav.) Sweet, 32, Nov. 191, found in an old disused native garden at Nongoma.
Hibiscus calyphyllus Cav., 136, Jan. 1912, found as an undershrub beneath larger trees near Amatohemphlope, 'Nhlwati.
Hibiscus cannabinus L., 71, Apr. 1911, found in the veld by an old mealie garden, Nongoma.
Hibiscus pedunculatus L., 159, April 1912, found in the bush at 'Nhlwati.
Hibiscus trionum L., 38, Dec. 1910, found in the veld among the long grass at Nongoma.
Pavonia columella Cav., 37, Dec. 1910, found on the site of an old disused mealie garden at Nongoma.
Sida rhombifolia L., 40, Dec. 1910, found in the veld at Nongoma.

OCHNACEAE
Ochna serrulata (Hochst.) Walp., 232, Oct. 1913, found in the veld by the Mona, near Nongoma road.

CLUSIACEAE
Hypericum aethiopicum Thunb., 228, Sept. 1913, found in the veld at Nongoma.

ONAGRACEAE
Oenothera rosea L'Hérit. ex Ait., 41, Dec. 1910, found as a weed in the garden at Isandhlwana.

GENTIANACEAE
Chironia krebsii Griseb., 25, Nov. 1910, found in the veld at 'Nhlwati.

APOCYNACEAE

Carissa bispinosa (L.) Brenan, 109, Oct. 1911, found in the bush at 'Nhlwati.

ASCLEPIADACEAE

Asclepias affinis (Schltr.) Schltr., 35, Nov. 1910, found in the veld at Nongoma.

Asclepias fruticosa L., 99, Sept. 1911, Umkuzana stream, near the Tokazi, Nongoma.

Asclepias physocarpa (E. Mey.) Schltr., 126, Nov. 1911, found in the veld at 'Nhlwati.

Aspidoglossum grandiflorum (Schultr.) Kupicha, 217, Aug. 1913), found on the roadside at 'Nhlwati.

Cynanchum natalitum Schltr., 255, July 1915, found in the bush at Dukumbane.

Raphionacme hirsuta (E. Mey.) R.A. Dyer & Phillips, 220, Aug. 1913, found in the veld at Nongoma.

Schizoglossum cordifolium E. Mey., 256, Aug. 1915, found in the veld at Nongoma.

Xysmalobium stockenstromense Scott-Elliot, 236, Nov. 1913, found in the veld at Nongoma.

Xysmalobium undulatum (L.) Ait. f., 241, Jan. 1914, found in the veld at Nongoma.

CONVOLVULACEAE

Convolvulus farinosus L., 57, Jan. 1911, found among the scrub by the roadside at Nongoma.

Convolvulus natalensis Bernh., 9, Sept. 1910, found in the veld at Nongoma.

Hewittia sublobata (L. f.) Kuntze, 180, Aug. 1912, found in an old mealie garden at 'Nhlwati.

Ipomoea ficifolia Lindl., 77, Apr. 1911, found growing as a weed in the garden at Nongoma.

Ipomoea obscura (L.) Ker-Gawl., 54, Jan. 1911, found in the veld at Nongoma.

Turbina oblongata (E. Mey. ex Choisy) A. Meeuse, 145, Feb. 1912, found in the veld at Nongoma.

LAMIACEAE

Hoslundia opposita Vahl, 274, Dec. 1915, found in the veld at Empangeni.

Leonotis leonurus (L.) R.Br., 213, July 1913, found in the veld at Kwamagwaza.

Leonotis ocymifolia (Burm. f.) Iwarsson, 70, Apr. 1911, found in the veld at Nongoma.

Orthosiphon serratus Schltr., 269, Oct. 1915, found in the veld at 'Nhlwati.

Plectranthus fruticosus L'Hérit., 283, Apr. 1916, found in the shade of thick bush at 'Nhlwati.

Pycnostachys urticifolia Hook., 210, June 1913, found in swampy ground in a donga at Nongoma.

Stachys sessilis Guerke, 261, Sept. 1915, found in the veld at Nongoma.

SOLANACEAE

Datura stramonium L., 160, April 1912, found as a weed in the garden at Nongoma.

Nicandra physaloides Gaertn., 51, Jan. 1911, found on the site of a disused garden at Nongoma.

Physalis peruviana L., 204, May 1913, found on some waste ground at 'Nhlwati.

Solanum aculeastrum Dun., 101, Sept. 1911, found on an old kraal site at Nongoma.

Solanum aculeatissimum Jacq., 246, Feb. 1914, found in the veld by the roadside at Nongoma.

Solanum coccineum Jacq., 154, March 1912, found on the edge of the bush at 'Nhlwati.

Solanum hermannii Dun., 107, Oct. 1911, found in the veld at Nongoma.

Solanum incanum L., 247, Feb. 1914, found on the roadside near Nongoma.

Solanum nigrum L., 103, Sept. 1911, found as a weed in garden at Nongoma.

Solanum panduriforme E. Mey., 115, Oct. 1911, found on waste ground round buildings at 'Nhlwati.

SCROPHULARIACEAE

Buchnera dura Benth., 120, Nov. 1911, found in the veld at 'Nhlwati.

Nemesia umbonata (Hiern) Hilliard & Burtt, 42, Dec. 1910, found in an old garden at Isandhlwana.

Striga asiatica (L.) Kuntze, 66, Mar. 1911, found in a mealie garden at Etaloneni.

SELAGINACEAE

Hebenstretia comosa Hochst., 218, Aug. 1913, found in the veld at 'Nhlwati.

Tetraselago natalensis (Rolfe) Junell, 75, Apr. 1911, found in the veld at Nongoma.

VERBENACEAE

Priva meyeri Jaub. & Spach, 123, Nov. 1911, found on some waste ground at 'Nhlwati.

BIGNONIACEAE

Kigelia africana (Lam.) Benth., 223, Sept. 1913, found on the banks of the Pongola River by the drift on Ubombo-Lugwavuma road.

Tecomaria capensis (Thunb.) Spach, 85, Oct. 23, 1908, found in the Umgeni bush near Durban.

GESNERIACEAE

Streptocarpus daviesii C.B. Cl., 48, Dec. 1910, found on a tree in Ngome forest.

LENTIBULARIACEAE

Utricularia livida E. Mey., 214, July 1913, found in a moist donga at Nongoma.

ACANTHACEAE

Crossandra greenstockii S. Moore, 21, Oct. 1910, found in the veld at Nongoma.

Justicia flava (Vahl) Vahl, 277, Jan. 1916, found in the veld by the roadside at Empangeni.

Justicia petiolaris C.B. Cl., 282, Apr. 1916, found in shady wood by the waterfall at 'Nhlwati.

Peristrophe natalensis T. Anders., 76, Apr. 1911, found among the long grass in the veld at Nongoma.

Ruellia cordata Thunb., 271, Nov. 1915, found in the veld at Nongoma.

Thunbergia atriplicifolia E. Mey., 106, Oct. 1911, found in the veld at Nongoma.

RUBIACEAE

Borreria scabra (Schumach. & Thonn.) K. Schum., 286, April 1916, found in the veld at 'Nhlwati.

Burchellia bubalina (L. f.) Sims, 113, Oct. 1911, found in the bush at 'Nhlwati.

Gardenia thunbergii L. f., 263, Sept. 1915, found in the bushveld near the Vuna on the Nongoma-Mahlabatini road.

Pentanisia prunelloides (Klotzsch ex Eckl. & Zeyh.) Walp., 215, Aug. 1913, found in the veld at Nongoma.

DIPSACACEAE

Scabiosa columbaria L., 178, July 1912, found in the veld at 'Nhlwati.

CUCURBITACEAE

Cucumis prophetarum L., 62, Feb. 1911, found in the veld at Nongoma.

Cucumis sp., 260, Sept. 1915, found in the veld at Empangeni.

CAMPANULACEAE

Lobelia erinus L., 5, Aug. 1910, found in the veld at Nongoma.

Lobelia sp., 224, Sept. 1913, found in the veld near the Swaziland border at Ingwavuma.

Monopsis decipiens (Sond.) Thulin, 100, Sept. 1911, found in the veld at Nongoma.

Monopsis stellarioides (Presl) Urb., 108, Oct. 1911, found by the stream at the waterfall at 'Nhlwati.

Wahlenbergia krebsii Cham. subsp. *krebsii*, 55, Jan. 1911, found in the veld at Nongoma.

GOODENIACEAE

Scaevola plumieri (L.) Vahl, 104, Oct. 28, 1908, found on the sand dunes on Durban foreshore.

ASTERACEAE

Aster bakerianus Burtt Davy ex C.A. Smith, 96, Aug. 1911, found in the veld at 'Nhlwati.

Athrixia phylicoides DC., 82, June 1911, found in the veld at Nongoma.

Berkheya insignis (Harv.) Thell., 31, Nov. 1910, found in the veld at Nongoma.

Bidens pilosa L., 87, July 1911, found as a weed in the garden at 'Nhlwati.

Callilepis laureola DC., 3, Aug. 1910, found in the veld at Nongoma.

Conyza canadensis (L.) Cronq., 227, Sept. 1913, found as a weed in the garden at Nongoma.

Dicoma anomala Sond., 74, Apr. 1911, found in the veld at Nongoma.

Dicoma argyrophylla Oliver, 219, Aug. 1913, found in the veld near the Mona stream on the Nongoma-Hlabisu road.

Dicoma speciosa DC., 64, Mar. 1911, found in the veld at Nongoma.

Gazania krebsiana Less., 185, Aug. 1912, found in the veld at 'Nhlwati.

Gerbera ambigua (Cass.) Schulz. Bip., 14, Sept. 1910, found in the veld at Nongoma.

Helichrysum adenocarpum DC., 162, April 1912, found in the veld at Ngome.

Helichrysum appendiculatum (L. f.) Less., 243, Feb. 1914, found in the veld at Nongoma.

Helichrysum cooperi Harv., 80, May 1911, found in the veld at Nongoma.

Helichrysum herbaceum (Andr.) Sweet, 174, July 1912, found in the veld at 'Nhlwati.

Helichrysum setosum Harv., 172, June 1912, found in the veld at 'Nhlwati.

Helichrysum umbraculigerum Less., 171, June 1912, found in the veld at 'Nhlwati.

Osteospermum grandidentatum DC., 186, Aug. 1912, found in the veld near 'Nhlwati.

Senecio deltoideus Less., 176, July 1912, found in the bush at 'Nhlwati.

Senecio erubescens Ait., 97, Aug. 1911, found in the veld at 'Nhlwati.

Sonchus integrifolius Harv., 83, Aug. 1912, found in an old mealie garden at 'Nhlwati.

Sonchus oleraceus L., 169, June 1912, found as a weed in the garden at Nongoma.

Vernonia hirsuta (DC.) Sch. Bip., 262, Sept. 1915, found in the veld at Nongoma.

Book Reviews

SOUTH WEST AFRICAN BOTANY by W. GIESS. 1989. Wissenschaftliche Forschung in Südwestafrika (18. Folge). *S.W.A. Wissenschaftliche Gesellschaft*, P.O. Box 67, Windhoek, Namibia. Pp. 236. Size 240 × 175 mm. ISBN 0-949995-46-0. Price: soft cover R35,00.

In the introduction to this work, the author gives a brief account of the historical development of botany in Namibia, taking the reader from the time of Thomas Baines in the second half of the 19th century, through the contributions of various other travellers, collectors, explorers, geologists and botanists, to Dr Hermann Merxmüller, author of the *Prodromus einer Flora von Südwestafrika* of which the last part was published in 1972.

The main part of the book is divided into two sections: the bibliography proper and a subject index. The bibliography is arranged alphabetically according to author, with references appearing in chronological order under the names of first authors. The names of co-authors are given in their alphabetical position, followed by a cross reference to the relevant first author.

The bibliography lists a total of 3 158 literature references, most of which have been drawn from the compiler's private library built up over more than 40 years and from reprints accumulated over 30 years' involvement with the S.W.A. Herbarium. As the author states in the introduction, the bibliography attempts to summarize the literature on Namibian plant life. However, the scope of the work has been intentionally broadened to include publications on related subjects such as climatology, soil science, vegetation studies, agricultural science and pasture science.

The publication contains references to books, journal articles, theses as well as a number of works 'not strictly scientific in nature' but containing information not found elsewhere. Where appropriate, titles of journals and series have been abbreviated, but book titles appear in full. The alphabetical subject index which follows the bibliography, lists mainly plant genera and families. However, it also enables the reader to find literature references on subjects such as animal diseases, chromosome studies, climate, expeditions, food plants, the Kalahari, mimicry plants, the Namib Desert, pasture research and precipitation. The index refers to the entries in the bibliography by their number.

The text has been produced on an unsophisticated dot-matrix printer giving the work an unprofessional look. Some letters, especially the italicized m, are blotched whereas others, like the italicized o and s, are broken. In the review copy, the print on a few pages is very light. The book has a soft cover carrying a pleasing colour photograph showing a few plants of *Pachypodium namaquanum* on a koppie overlooking a vast plain somewhere in the south of Namibia.

In the preface, Mr M.A.N. Müller of the S.W.A. Herbarium in Windhoek mentions the 'long-felt need by those involved in the study of South West African plants' for a bibliography of this kind. I am sure that botanists and other scientists concerned with Namibian plants and their environment, will find Mr Giess's book a most useful tool.

EMSIE DU PLESSIS

FLORA OF SOUTH-EASTERN QUEENSLAND VOL. III by T.D. STANLEY and E.M. ROSS. 1989. *Queensland Department of Primary Industries* Miscellaneous Publication QM88001, G.P.O. Box 46, Brisbane 4001, Australia. Pp. 532, 64 plates. Price: hard cover: $40.

This is the third and final volume in the series, *Flora of South-eastern Queensland*, in which the monocotyledons and Gymnospermae are treated. The families are arranged according to Hutchinson's classification (1959). Forty-seven families, 324 genera and 1 114 species are dealt with, including 200 introduced taxa. No less than 137 of these are Poaceae, originally introduced as pasturage. Many are southern African.

The first two volumes in the series, treating the dicotyledons, were published in 1983 and 1986 respectively. Vol. 1 was reviewed in *Bothalia* 21,1: 115 (1991) and Vol. II was reviewed in *Bothalia* 21,2: 227 (1991). It is unneccessary to repeat the description and comments provided by the previous reviewers, apart from mentioning that once again cumulative indexes to scientific and common names are included.

The composite plates, however, deserve further comment. Several artists contributed to this volume and it is interesting to contrast their styles. Unfortunately some plates are rather disappointing, especially of Poaceae and Orchidaceae, with the same thick pen being used for structural, textural and shading lines, the overall effect being flat and very black. By way of contrast the plates of Juncaceae, Restionaceae and Cyperaceae are beautiful, although some of the latter do suffer from over-reduction.

The overall presentation of this volume is pleasing, with an attractive cover design featuring one of the included species. The avoidance of highly technical terminology should ensure that this Flora will find a market amongst students and interested members of the public.

C. REID

Bothalia 22,1: 157–164 (1992)

Guide for authors to Bothalia

This guide is updated when necessary and includes an index. The latest version should therefore be consulted.

Bothalia is named in honour of General Louis Botha, first Premier and Minister of Agriculture of the Union of South Africa. This house journal of the National Botanical Institute, Pretoria, is devoted to the furtherance of botanical science. The main fields covered are taxonomy, ecology, anatomy and cytology. Two parts of the journal and an index to contents, authors and subjects are published annually.

1 Editorial policy

Bothalia welcomes original papers dealing with flora and vegetation of southern Africa and related subjects. Full-length papers and short notes, as well as book reviews, are accepted. Manuscripts may be written in either English or Afrikaans.

Articles are assessed by referees, both local and overseas. Authors are welcome to suggest possible referees to judge their work. Authors are responsible for the factual correctness of their contributions. *Bothalia* maintains an editorial board (see title page) to ensure that international standards are upheld.

Articles should preferably be submitted on PC diskettes or stiffies but the format of all articles should conform to paragraphs 3.2 to 3.5. Articles not submitted in electronic form should be arranged according to section 3.

2 Requirements for a diskette

2.1 data must be IBM compatible and written in ASCII.

2.2 a printout of the diskette should be supplied to indicate (**in pencil**) the necessary underlining, paragraphs etc.

2.3 tables need not be placed on the diskette—a typed version is adequate.

2.4 the diskette must have single line spacing, the printout with markings must be in double line spacing.

2.5 do not justify lines.

2.6 do not break words, except hyphenated words.

2.7 all lines, headings, keys, etc., should start flush at the margin, therefore no indentations of any kind.

2.8 no italics, bold or underlined words.

2.9 paragraphs and headings are delineated by an extra line spacing (carriage return) and no indentation.

2.10 a hyphen is designated as one dash, with no space between the letter and the dash, e.g. ovate-lanceolate. See also 17.6.

2.11 an N-dash is typed as two hyphens with no space between the letter and the hyphen, e.g. 2--5 mm (typeset, it looks like this, 2–5 mm).

2.12 an M-dash is typed as three hyphens with no space between the letter and the hyphen, e.g. computers---what a blessing! (typeset, it looks like this, computers—what).

2.13 do not use a double space between words, after commas, full stops, colons, semicolons or exclamation marks.

2.14 use lower case x as a times sign, with one space on either side of the x, e.g. 2 x 3 mm.

2.15 use single (not double) opening and closing quotes.

2.16 keys—put only three leader dots before number and name of taxon (with a space before and a space after the first and last dot), regardless of how far or near the word is from the right margin, e.g. ... 1. *R. ovata*.

3 Requirements for a manuscript

3.1 Manuscripts should be typewritten on one side of good quality A4-size paper, double-spaced throughout (including abstract, tables, captions to figures, literature references, etc.) and have a margin of at least 30 mm all round. The original and three photocopies (preferably **photocopied on both sides** of the paper to reduce weight for postage) of all items, including text, illustrations, tables and lists should be submitted, and the author should retain a complete set of copies.

3.2 Papers should conform to the general style and layout of recent issues of *Bothalia* (from volume 17 onwards).

3.3 Material should be presented in the following sequence: Title page with title, name(s) of author(s), keywords, abstracts (in English and Afrikaans) and information that should be placed in a footnote on the title page, such as address(es) of author(s) and mention of granting agencies.

3.4 The sequence continues with Introduction and aims, Material and methods, Results, Interpretation (Discussion), Acknowledgements, Specimens examined (in revisions and monographs), References, Index of names (recommended for revisions dealing with more than about 15 species), Tables, Captions for figures and figures. In the case of short notes and book reviews, keywords and abstract are superfluous.

3.5 All pages must be numbered consecutively beginning with the title page to those with references, tables and captions to figures.

3.6 For notes on the use of hyphens and dashes see 2.10 to 2.12.

4 Author(s)

When there are several authors the covering letter should indicate clearly which of them is responsible for correspondence and, if possible, telephonically available while the article is being processed. The contact address and telephone number should be mentioned if they differ from those given on the letterhead.

5 Title

The title should be as concise and as informative as possible. In articles dealing with taxonomy or closely related subjects the family of the taxon under discussion (see also 13.2) should be mentioned in brackets but author citations should be omitted from plant names.

6 Keywords

Up to 10 keywords (or index terms) should be provided in English in alphabetical sequence. The following points should be borne in mind when selecting keywords:

6.1 Keywords should be unambiguous, internationally acceptable words and not recently-coined little-known words.

6.2 they should be in a noun form and verbs should be avoided.

6.3 they should not consist of an adjective alone; adjectives should be combined with nouns.

6.4 they should not contain prepositions.

6.5 the singular form should be used for processes and properties, e.g. evaporation.

6.6 the plural form should be used for physical objects, e.g. augers.

6.7 location (province and/or country); taxa (species, genus, family) and vegetation type (community, veld type, biome) should be used as keywords.

6.8 keywords should be selected hierarchically where possible, e.g. both family and species should be included.

6.9 they should include terms used in the title.

6.10 they should answer the following questions:

6.10.1 what is the *active concept* in the document (activity, operation or process).

6.10.2, what is the *passive concept* or object of the active process (item on which the activity, operation or process takes place).

6.10.3, what is the means of accomplishment or how is the active concept achieved (technique, method, apparatus, operation or process).

6.10.4 what is the environment in which the active concept takes place (medium, location).

6.10.5 what are the independent (controlled) and dependent variables?

6.11 questions 6.10.1 to 6.10.3 should preferably also be answered in the title.

7 Abstract

7.1 Abstracts of no more than 200 words should be provided in English and Afrikaans. Abstracts are of great importance and should convey the essence of the article.

7.2 They should refer to the geographical area concerned and, in taxonomic articles, mention the number of taxa treated. They should not contain information not appearing in the article.

7.3 In articles dealing with taxonomy or closely related subjects all taxa from the rank of genus downwards should be accompanied by their author citations.

7.4 Names of new taxa and new combinations should not be underlined. If the article deals with too many taxa only the important ones should be mentioned.

8 Table of contents

A table of contents should be given for all articles longer than about six typed pages, unless they follow the strict format of a taxonomic revision.

9 Acknowledgements

Acknowledgements should be kept to the minimum compatible with the requirements of courtesy. Please give all the initials of the person(s) you are thanking.

10 Literature references

10.1 Literature references in the text should be cited as follows: 'Jones & Smith (1986) stated...', or '...(Jones & Smith 1986)' or (Ellis 1988: 67) when giving a reference simply as authority for a statement. For treatment of literature references in taxomonic papers see 14.

10.2 When more than two authors are involved in the paper use the name of the first author followed by *et al.*

10.3 When referring to more than one literature reference, they should be arranged alphabetically according to author and separated by a semicolon, e.g. (Anon. 1981, 1984; Davis 1976; Nixon 1940).

10.4 Titles of books and names of journals should preferably not be mentioned in the text. If there is good reason for doing so, they should be treated as described in 10.12 & 10.13.

10.5 Personal communications are given only in the text, not in the list of references. Please add the person's full initials to identify the person more positively, e.g. C. Boucher pers. comm.

10.6 References of the same author are arranged in chronological sequence.

10.7 Where two or more references by the same author are listed in succession, the author's name is repeated with every reference.

10.8 All publications referred to in the text, including those mentioned in full in the treatment of correct names in taxonomic papers, but no others, and no personal communications, are listed at the end of the manuscript under the heading References.

10.9 The references are arranged alphabetically according to authors and chronologically under each author, with a, b, c, etc. added to the year, if the author has published more than one work in a year.

10.10 If an author has published both on his own and as a senior author with others, the solo publications are listed first and after that, in strict alphabetical sequence, those published with one or more other authors.

10.11 Author names are typed in capitals.

10.12 Titles of journals and of books are written out in full and are underlined as follows: *Transactions of the Linnean Society of London* 5: 171–217, or *Biology and ecology of weeds*: 24.

10.13 Titles of books should be given as in *Taxonomic literature*, edn 2 by Stafleu & Cowan and names of journals as in the latest edition of *World list of scientific periodicals*.

10.14 If the same author is mentioned more than once, the name is written out in full and not replaced by a line.

10.15 Examples of references:

Collective book or Flora

BROWN, N.E. 1909. Asclepiadaceae. In W.T. Thiselton-Dyer, *Flora capensis* 6,2: 518–1036. Reeve, London.
BROWN, N.E. 1915. Asclepiadaceae. In W.T. Thiselton-Dyer, *Flora of tropical Africa* 5,2: 500–600. Reeve, London.

Book

DU TOIT, A.L. 1966. *Geology of South Africa*, 3rd edn, S.M. Haughton (ed.). Oliver & Boyd, London.
HUTCHINSON, J. 1946. *A botanist in southern Africa*. Gawthorn, London.

Journal

DAVIS, G. 1988. Description of a proteoid-restioid stand in Mesic Mountain Fynbos of the south-western Cape and some aspects of its ecology. *Bothalia* 18: 279–287.
STEBBINS, G.L. Jr 1952. Aridity as a stimulus to plant evolution. *American Naturalist* 86: 35–44.
SMOOK, L. & GIBBS RUSSELL, G.E. 1985. Poaceae. *Memoirs of the Botanical Survey of South Africa* No. 51: 45–70.

In press, in preparation

TAYLOR, H.C. in press. *A reconnaissance of the vegetation of Rooiberg State Forest*. Department of Forestry, Technical Bulletin.
VOGEL, J.C. 1982. The age of the the Kuiseb river silt terrace at Homeb. *Palaeoecology of Africa* 15. In press.
WEISSER, P.J., GARLAND, J.F. & DREWS, B.K. in prep. Dune advancement 1937–1977 and preliminary vegetation succession chronology at Mlalazi Nature Reserve, Natal, South Africa. *Bothalia*.

Thesis

KRUGER, F.J. 1974. *The physiography and plant communities of the Jakkalsrivier Catchment*. M.Sc. (Forestry) thesis, University of Stellenbosch.

Miscellaneous paper, report, unpublished article, technical note, congress proceedings

ANON. no date. *Eetbare plante van die Wolkberg*. Botanical Research Unit, Grahamstown. Unpublished.
BAWDEN, M.G. & CARROL, D.M. 1968. *The land resources of Lesotho*. Land Resources Study No. 3, Land Resources Division, Directorate of Overseas Surveys, Tolworth.
BOUCHER, C. 1981. Contributions of the Botanical Research Institute. In A.E.F. Heydorn, *Proceedings of workshop research in Cape estuaries*: 105–107. National Research Institute for Oceanology, CSIR, Stellenbosch.
NATIONAL BUILDING RESEARCH INSTITUTE 1959. *Report of the committee on the protection of building timbers in South Africa against termites, woodboring beetles and fungi*, 2nd edn, CSIR Research Report No. 169.

11 Tables

11.1 Each table should be presented on a separate sheet and be assigned an Arabic numeral, i.e. the first table mentioned in the text is marked 'Table 1'.

11.2 In the captions of tables the word 'table' is written in capital letters. See recent numbers of *Bothalia* for the format required.

11.3 Avoid vertical lines, if at all possible. Tables can often be reduced in width by interchanging primary horizontal and vertical heads.

12 Figures

12.1 Figures should be planned to fit, after reduction, into a width of either 80, 118 or 165 mm, with a maximum vertical length of 230 mm. Allow space for the caption in the case of figures that will occupy a whole page.

12.2 Line drawings, including graphs and diagrams, should be in jet-black Indian ink, preferably on fine Felix Schoeller parole or similar board, 200 gsm, or tracing film. Lines should be bold enough to stand reduction.

12.3 It is recommended that drawings should be twice the size of the final reproduction.

12.4 Photographs should be of excellent quality on glossy paper with clear detail and moderate contrast, and they should be the same size as required in the journal.

12.5 Photograph mosaics should be submitted complete, the component photographs mounted neatly on a white flexible card base leaving a narrow gap of uniform width (2 mm) between each print. Note that grouping photographs of markedly divergent contrast results in poor reproductions.

12.6 Lettering and numbering on all figures should be done in letraset, stencilling or a comparable method. If symbols are to be placed on a dark background it is recommended that black symbols are used on a small white disk ± 7 mm in diameter and placed in the lower left hand corner of the relevant photo.

12.7 If several illustrations are treated as components of a single composite figure they should be designated by capital letters.

12.8 Note that the word 'figure' should be written out in full, both in the text and the captions.

12.9 In the text the figure reference is then written as in the following example: 'The stamens (Figure 4A, B, C) are...'

12.10 In captions, 'figure' is written in capital letters. Magnification of figures should be given for the size as submitted.

12.11 It is recommended that scale bars or lines be used on figures.

12.12 In figures accompanying taxonomic papers, voucher specimens should be given in the relevant caption.

12.13 Figures are numbered consecutively with Arabic numerals in the order they are referred to in the text. These numbers, as well as the author's name and an indication of the top of the figure, must be written in soft pencil on the back of all figures.

12.14 Captions of figures must not be pasted under the photograph or drawing.

12.15 Authors should indicate in pencil in the text where they would like the figures to appear.

12.16 Authors wishing to have the originals of figures returned must inform the editor in the original covering letter and must mark each original 'To be returned to author'.

12.17 Authors wishing to use illustrations already published must obtain written permission before submitting the manuscript and inform the editor of this fact.

12.18 Captions for figures should be collected together and typed on a separate sheet headed *Captions for figures*.

12.19 It is strongly recommended that taxonomic articles include dot maps as figures to show the distribution of taxa. The dots used must be large enough to stand reduction to 80 mm (recommended size: letraset 5 mm diameter).

12.20 Blank maps are available from the editor.

13 Text

13.1 As a rule authors should use the names as listed by Gibbs Russell *et al.* in *Memoirs of the Botanical Survey of South Africa* Nos 48, 51 and 56.

13.2 Names of genera and infrageneric taxa are usually underlined, with the author citation (where relevant) not underlined. Exceptions include names of new taxa in the abstracts, correct names given in the synopsis or in paragraphs on species excluded from a given supraspecific group in taxonomic articles, in checklists and in indices, where the position is reversed, correct names not being underlined and synonyms underlined.

13.3 Names above generic level are not underlined.

13.4 In articles dealing with taxonomy and closely related subjects the complete scientific name of a plant (with author citation) should be given at the first mention in the text. The generic name should be abbreviated to the initial thereafter, except where intervening references to other genera with the same initial could cause confusion.

13.5 In normal text, Latin words are italicized, but in the synopsis of a species, Latin words such as *nom. nud.* are not italicized.

13.6 Names of authors of plant names should agree with the list compiled by the BRI (TN TAX 2/1) which has also been implemented by Gibbs Russell *et al.* in *Memoirs of the Botanical Survey of South Africa* Nos 48, 51 and 56.

13.7 Modern authors not included in the list should use their full name and initials when publishing new plant names. Other author names not in the list should be in agreement with the recommendations of the Code.

13.8 Names of authors of publications are written out in full except in the synonymy in taxonomic articles where they are treated like names of authors of plant names.

13.9 Names of plant collectors are underlined whenever they are linked to the number of a specimen. The collection number is also underlined, e.g. *Acocks 14407.*

13.10 Surnames beginning with 'De', 'Du' or 'Van' begin with a capial letter unless preceded by an initial.

13.11 For measurements use only units of the International System of Units (SI). Cm should not be used, only mm and/or m.

13.12 The use of '±' is preferred to c. or ca.

13.13 Numbers 'one' to 'nine' are spelled out in normal text, and from 10 onwards they are written in Arabic numerals.

13.14 In descriptions of plants, numerals are used throughout. Write 2.0–4.5 (not 2–4.5). When counting members write 2 or 3 (not 2–3) but 2–4.

13.15 Abbreviations should be used sparingly but consistently. No full stops are placed after abbreviations ending with the last letter of the full word (e.g. edition = edn; editor = ed.), after units of measure, after compass directions and after herbarium designations.

13.16 Apart from multi-access keys, indented keys should be used with couplets numbered la–lb, 2a–2b, etc. (without full stops thereafter).

13.17 Keys consisting of a single couplet have no numbering.

13.18 Manuscripts of keys should be presented as in the following example:

la Leaves closely arranged on an elongated stem; a submerged aquatic with only the capitula exserted ... lb. *E. setaceum* var. *pumilum*

lb Leaves in basal rosettes; stems suppressed; small marsh plants, ruderals or rarely aquatics:

2a Annuals, small, fast-growing pioneers, dying when the habitat dries up; capitula without coarse white setae; receptacles cylindrical:

3a Anthers white ... 2. *E. cinereum*

3b Anthers black ... 3. *E. nigrum*

2b Perennials, more robust plants; capitula sparsely to densely covered with short setae:

13.19 Herbarium voucher specimens should be referred to wherever possible, not only in taxonomic articles.

14 Species treatment in taxonomic papers

14.1 The procedure to be followed is illustrated in the example (17, 17.8), which should be referred to, because not all steps are described in full detail.

14.2 The correct name (not underlined) is to be followed by its author citation (underlined) and the full literature reference, with the name of the publication written out in full (not underlined).

14.3 Thereafter all literature references, including those of the synonyms, should only reflect author, page and year of publication, e.g. C.E. Hubb. in Kew Bulletin 15: 307 (1960); Boris *et al.*: 14 (1966); Boris: 89 (1967); Sims: t. 38 (1977); Sims: 67 (1980).

14.4 The description and the discussion, which should consist of paragraphs commencing, where possible, with italicized leader words such as *flowering time, diagnostic characters, distribution* and *habitat.*

14.5 When more than one species of a given genus is dealt with in a paper, the correct name of each species should be prefixed by a sequential number followed by a full stop, the first line of the paragraph to be indented. Infraspecific taxa are marked with small letters, e.g. lb., 12c., etc.

14.6 Names of authors are written in the same way (see 13.1, 13.6), irrespective of whether the person in question is cited as the author of a plant name or of a publication.

14.7 The word 'figure' is written as 'fig.', and 't.' is used for both 'plate' and 'tablet'.

14.8 Literature references providing good illustrations of the species in question may be cited in a paragraph commencing with the word Icones followed by a colon. This paragraph is given after the last paragraph of the synonymy, see 17.8.

15 Citation of specimens

15.1 Type specimen in synopsis: the following should be given (if available): country (if not in RSA), province, grid reference (at least for new taxa), locality as given by original collector, modern equivalent of collecting locality in square brackets (if relevant), date of collection (optional), collector's name and collecting number (both underlined).

15.2 The abbreviation *s.n.* (*sine numero*) is given after the name of a collector who usually assigned numbers to his collections but did not do so in the specimen in question. The herbaria in which the relevant type(s) are housed are indicated by means of the abbreviations given in the latest edition of *Index Herbariorum*.

15.3 The holotype (holo.) and its location are mentioned first, followed by a semicolon, the other herbaria are arranged alphabetically, separated by commas.

15.4 Authors should indicate by means of an exclamation mark (!) which of the types have been personally examined.

15.5 If only a photograph or microfiche was seen, write as follows: *Anon. 422* (X, holo.—BOL, photo.!).

15.6 Lectotypes or neotypes should be chosen for correct names without a holotype. It is not necessary to lectotypify synonyms.

15.7 When a lectotype or a neotype are newly chosen this should be indicated by using the phrase 'here designated'. If reference is made to a previously selected lectotype or neotype, the name of the designating author and the literature reference should be given. In cases where no type was cited, and none has subsequently been nominated, this may be stated as 'not designated'.

15.8 In brief papers mentioning only a few species and a few cited specimens the specimens should be arranged according to the grid reference system: Provinces/countries (typed in capitals) should be cited in the following order: SWA/Namibia, Botswana, Transvaal, Orange Free State, Swaziland, Natal, Lesotho, Transkei and Cape.

15.9 Grid references should be cited in numerical sequence.

15.10 Locality records for specimens should preferably be given to within a quarter-degree square. Records from the same one-degree square are given in alphabetical order, i.e (—AC) precedes (—AD), etc. Records from the same quarter-degree square are arranged alphabetically according to the collectors' names; the quarter-degree references must be repeated for each specimen cited.

15.11 The relevant international code of the herbaria in which a collection was seen should be given in brackets after the collection number; the codes are separated by commas. The following example will explain the procedure:

NATAL.—2731 (Louwsburg): 16 km E of Nongoma, (—DD), *Pelser 354* (BM, K, PRE); near Dwarsrand, *Van der Merwe 4789* (BOL, M). 2829 (Harrismith): near Groothoek, (—AB), *Smith 234*; Koffiefontein, (—AB), *Taylor 720* (PRE); Cathedral Peak Forest Station, (—CC), *Marriot 74* (KMG); Wilgerfontein, *Roux 426*. Grid ref. unknown: Sterkstroom, *Strydom 12* (NBG).

15.12 For records from outside southern Africa authors should use degree squares without names, e.g.:

KENYA.—0136: Nairobi plains beyond race course, *Napier 485*.

15.13 Monographs and revisions: in the case of all major works of this nature it is assumed that the author has investigated the relevant material in all major herbaria and that he has provided the specimens seen with determinavit labels. It is assumed further that the author has submitted distribution maps for all relevant taxa and that the distribution has been described briefly in words in the text. Under the heading 'Vouchers' no more than five specimens should be cited, indicating merely the collector and the collector's number (both underlined). Specimens are alphabetically arranged according to collector's name. If more than one specimen by the same collector is cited, they are arranged numerically and separated by a semicolon. The purpose of the cited specimens is not to indicate distribution but to convey the author's concept of the taxon in question.

15.14 The herbaria in which the specimens are housed are indicated by means of the abbreviation given in the latest edition of *Index Herbariorum*. They are given between brackets, arranged alphabetically and separated by commas behind every specimen as in the following example:

Vouchers: *Fisher 840* (NH, NU, PRE); *Flanagan 831* (GRA, PRE); *840* (NH(PRE); *Marloth 4926* (PRE, STE); *Schelpe 6161, 6163, 6405* (BOL); *Schlechter 4451* (BM, BOL, GRA, K, PRE).

15.15 If long lists of specimens are given, they should be listed together at the end of the article under the heading *Specimens examined*. They are arranged alphabetically by the collector's name and then numerically for each collector. The species is indicated in brackets by the number that was assigned to it in the text and any infraspecific taxa by a small letter. If more than one genus is dealt with in a given article, the first species of the first genus mentioned is indicated as 1.1. This is followed by the international herbarium designation. Note that the name of the collector and the collection number are underlined:

Acocks 12497 (2.1b) BM, K, PRE; *14724* (1.13a) BOL, K, P. *Archer 1507* (1.4) BM, G.

Burchell 2847 (2.8c) MB, K. *Burman 2401* (3.3) MO, S. *Burtt 789* (2.6) B, KMG, STE.

16 Synonyms

16.1 In a monograph or a revision covering all of southern Africa, all synonyms based on types of southern African origin, or used in southern African literature, should be included.

16.2 Illegitimate names are designated by *nom. illeg.* after the reference, followed by *non* with the author and date, if there is an earlier homonym.

16.3 *Nomina nuda* (*nom. nud.*) and invalid names are excluded unless there is a special reason to cite them, for example if they have been used in prominent publications.

16.4 In normal text Latin words are italicized, but in the synopsis of a species Latin words such as *nom. nud.* are not italicized.

16.5 Synonyms should be arranged chronologically into groups of nomenclatural synonyms, i.e. synonyms based on the same type, and the groups should be arranged chronologically by basionyms, except for the basionym of the correct name which is dealt with in the paragraph directly after that of the correct name.

16.6 When a generic name is repeated in a given synonymy it should be abbreviated to the initial except where intervening references to other genera with the same initial could cause confusion.

17 Description and example of species treatment

17.1 Descriptions of all taxa of higher plants should, where possible, follow the sequence: Habit; sexuality; underground parts (if relevant). *Indumentum* (if it can be easily described for the whole plant). *Stems/branches. Bark. Leaves*: arrangement, petiole absent/present, pubescence; blade: shape, size, apex, base, margin; midrib: above/below, texture, colour; petiole; stipules. *Inflorescence*: type, shape, position; bracts/bracteoles. *Flowers*: shape, sex. *Receptacle. Calyx. Corolla. Disc. Androecium. Gynoecium. Fruit. Seeds. Chromosome number.* Figure (word written out in full) number.

17.2 As a rule shape should be given before measurements.

17.3 In general, if an organ has more than one of the parts being described, use the plural, otherwise use the singular, for example, petals of a flower but blade of a leaf.

17.4 Language must be as concise as possible, using participles instead of verbs.

17.5 Dimension ranges should be cited as in the example below.

17.6 Care must be exercised in the use of dashes and hyphens: a *hyphen* is a short stroke joining two syllables of a word, e.g. ovate-lanceolate or sea-green, with no space between the letter and the stroke; an *N-dash* (*en*) is a longer stroke commonly used instead of the word 'to' between numerals, '2–5 mm long' (do not use it between words but rather use the word 'to', e.g. 'ovate to lanceolate'); it is produced by typing 2 hyphens next to each other; and an *M-dash* (*em*) is a stroke longer than an N-dash and is used variously, e.g. in front of a subspecific epithet instead of the full species name; it is produced by typing 3 hyphens next to one another.

17.7 The use of '±' is preferred to c. or ca when describing shape, measurements, dimensions, etc.

17.8 **The decimal point replaces the comma in all units of measurement** e.g. leaves 1.0–1.5 mm long.

17.9 Example:

1. **Bequaertiodendron magalismontanum** *(Sond.) Heine & Hemsl.* in Kew Bulletin: 307 (1960); Codd: 72 (1964); Elsdon: 75 (1980). Type: Transvaal, Magaliesberg, *Zeyher 1849* (S, holo.–BOL, photo.!).

Chrysophyllum magalismontanum Sond.: 721 (1850); Harv.: 812 (1867); Engl.: 434 (1904); Bottmar: 34 (1919). *Zeyherella magalismontanum* (Sond.) Aubrév. & Pelegr.: 105 (1958); Justin: (1973).

Chrysophyllum argyrophyllum Hiern: 721 (1850); Engl.: 43 (1904). *Boivinella argyrophylla* (Hiern) Aubrév. & Pellegr.: 37 (1958); Justin: 98 (1973). Types: Angola, *Welwitsch 4828* (BM!, lecto., here designated; PRE!); Angola, *Welwitsch 4872* (BM!).

Chrysophyllum wilmsii Engl.: 4, t. 16 (1904); Masonet: 77 (1923); Woodson: 244 (1937). *Boivinella wilmsii* (Engl.) Aubrév. & Pellegr.: 39 (1958); Justin: 99 (1973). Type: Transvaal, Magoebaskloof, *Wilms 1812* (B, holo.; K!, P!, lecto., designated by Aubrév. & Pellegr.: 38 (1958), PRE!, S!, W!, Z!).

Bequaertiodendron fruticosa De Wild.: 37 (1923), non Bonpland: 590 (1823); Bakker: 167 (1929); Fries: 302 (1938); Davy: 640 (1954); Breytenbach: 117 (1959); Clausen: 720 (1968); Pelmer: 34 (1969). Type: Transvaal, Tzaneen Distr., *Granville 3665* (K, holo.!; G!, P!, PRE!, S!).

Bequaertiodendron fragrans auct. non Oldemann: Glover: 149, t. 19 (1915); Henkel: 226 (1934); Stapelton: 6 (1954).

Icones: Harv.: 812 (1867); Henkel: t. 84 (1934); Codd: 73 (1964); Palmer: 35 (1969).

Woody perennial; main branches up to 0.4 m long, erect or decumbent, grey woolly-felted, leafy. *Leaves* 3–10(–23) × 1.0–1.5(–4.0) mm, linear to oblanceolate, obtuse, base broad, half-clasping. *Heads* heterogamous, campanulate, 7–8 × 5 mm, solitary, sessile at tip of axillary shoots; involucral bracts in 5 or 6 series, inner exceeding flowers, tips subopaque, white, very acute. *Receptacle* nearly smooth. *Flowers* ± 23–30, 7–11 male, 16–21 bisexual, yellow, tipped pink. *Achenes* ± 0,75 mm long, elliptic. *Pappus* bristles very many, equalling corolla, scabridulous. *Chromosome number*: 2n = 22. Figure 23B.

18 New taxa

18.1 The name of a new taxon must be accompanied by at least a Latin diagnosis. Authors should not provide full-length Latin descriptions unless they have the required expertise in Latin at their disposal.

18.2 It is recommended that descriptions of new taxa be accompanied by a good illustration (line drawing or photograph) and a distribution map.

18.3 Example:

109. **Helichrysum jubilatum** *Hilliard*, sp. nov. *H. alsinoidei* DC. affinis, sed foliis ellipticis (nec spatulatis), inflorescentiis compositis a foliis non circumcinctis, floribus femineis numero quasi dimidium hermaphroditorium aequantibus (nec capitulis homogamis vel floribus femineis 1–3 tantum) distinguitur.

Herba annua e basi ramosa; caules erecti vel decumbentes, 100–250 mm longi, tenuiter albo-lanati, remote foliati. *Folia* plerumque 8–30 × 5–15 mm, sub capitulis minora, elliptica vel oblanceolata, obtusa vel acuta, mucronata, basi semi-amplexicauli, utrinque cano-lanato-arachnoidea. *Capitula* heterogama, campanulata, 3.5–4.0 × 2.5 mm, pro parte maxima in paniculas cymosas terminales aggregata; capitula subterminalia interdum solitaria vel 2–3 ad apices ramulorum nudorum ad 30 mm longorum. *Bracteae involucrales* 5-seriatae, gradatae, exteriores pellucidae, pallide stramineae, dorso lanatae, seriebus duabus interioribus subaequalibus et flores quasi aequantibus, apicibus obtusis opacis niveis vix radiantibus. *Receptaculum* fere laeve. *Flores* ± 35–41. *Achenia* 0.75 mm longa, pilis myxogenis praedita. *Pappi* setae multae, corollam aequantes, apicibus scabridis, basibus non cohaerentibus.

TYPE.—Cape, 2817 (Vioolsdrif): (−CC), Richtersveld, ± 5 miles E of Lekkersing on road to Stinkfontein, kloof in hill south of road, annual, disc whitish, 7.11.1962, *Nordenstam 1823* (S, holo.; E, NH, PRE).

19 Proofs

Only page proofs are normally sent to authors. They should be corrected in red ink and be returned to the editor **as soon as possible**.

20 Reprints

Authors receive 100 reprints free. If there is more than one author, this number will have to be shared between them.

21 Documents consulted

Guides to authors of the following publications were made use of in the compilation of the present guide: *Annals of the Missouri Botanic Garden, Botanical Journal of the Linnean Society, Flora of Australia, Smithsonian Contributions to Botany, South African Journal of Botany* (including instructions to authors of taxonomic papers), *South African Journal of Science.*

22 Address of editor

Manuscripts should be submitted to: The Editor, Bothalia, National Botanical Institute, Private Bag X101, Pretoria 0001.

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